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TREE GROWTH

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THE BOTANICAL REVIEW

VOL. XXI JANUARY–MARCH, 1955 NOS. 1–3

TREE GROWTH

I. Some Historical Chapters

R. A. STUDHALTER[1]

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"Fraget die Bäume! Besser als alle Bücherweisheit werden sie euch sagen, wie sie behandelt sein wollen".

—Theodor Hartig

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INTRODUCTION

Observations on the manner in which trees carry on the processes of growth must have antedated the historic era; the sequence from seed to germination, to seedling, to sapling, and from young tree to mature tree must have been observed by primitive man in all parts of the world, even before the Stone Age. Also lost in the fogs of prehistory are the first observations on the annual length growth of branches and on the formation of growth "rings" in the wood, although there can be no doubt that these phenomena, too, were observed if not understood in very early times.

[1] Sincere thanks are given to Mr. R. C. Janeway, Librarian, Texas Technological College, for his understanding help in making available through interlibrary loan many hundreds of books and articles which could not otherwise have been examined, and to the Bibliographical Center for Research at Denver, Colorado, for processing a large part of these loans.

The mists of early written history are almost as impenetrable as are the fogs of prehistory. What was known by the several early civilizations which ranged all the way from China to the Nile and which covered a period of several millenia, is virtually a blank page to us. They do not seem to have left records of any knowledge whatsoever of the growth of plants. And some writings, known once to have existed, have been lost. Thus Aristotle's works are said (Kieser, 1812) to contain some fragmentary references to botanical writings by the Greek author Empedocles of Agrigentum (c. 450 B.C.) who was perhaps the first, at least in the western world, to have written on botanical subjects.

The present historical review is intended less as a complete history of our knowledge of the growth of trees than as a record, in a large measure forgotten today, of the early development of certain fundamental ideas; in other cases, new interpretations are given to some well-known subjects.

THEORY OF BUD-ROOTS

The earliest written observation on the growth of trees which has come to our attention occurs in a Hippocratic collection, discussed in Cohen and Drabkin (1948). The date of this collection is not given but, if not written by Hippocrates himself (c. 450–357 B.C.), it probably lies between his time and that of Aristotle (384–322 B.C.). Quoting: "Now if buds are taken from trees and inserted into other trees, and, becoming trees themselves, live on these other trees and bear fruit, the fruit is unlike that of the trees upon which they have been grafted. This comes about as follows. First the bud sprouts, for it has nourishment originally from the tree from which it was taken and then in that upon which it was grafted. When it has sprouted in this way it sends out tender roots to the tree and at first derives nourishment from the moisture of the tree upon which it has been grafted. Then after a time it sends roots into the ground through the tree upon which it has been grafted and derives nourishment from the soil, drawing up moisture. It is from this source that it is fed. Hence one should not be surprised to find that grafts bear fruit different from that of the trees upon which they are grafted. For they live from the earth". The term "grafting" is here used in its broader sense to include budding. E. H. F. Meyer (1854, Vol. 1) and

Unger (1855) refer to this theory under writings called Pseudo-Hippocrates, dated 424 B.C. A. Braun (1853) stated that Moquin-Tandon, in his "Teratologie", cited Hippocrates on individuality in plants.

This very early hypothesis, here applied to the artificial process of budding, was soon to be used as an explanation of the natural growth of buds on trees and shrubs, to become extended in its scope and details, and to be claimed as an original theory by several later botanists, even into the nineteenth century. It has been called the "theory of descending vessels" and "the theory of phytons", in addition to "the bud-root theory".

Whether Aristotle himself wrote a treatise on botany is not certain; he is given credit for discussing individuality of buds and branches by Schulz (date?) and by Wimmer (1838). His pupil and successor, Theophrastus of Eresus (c. 372–287 B.C.), wrote voluminously on the science of plants; just how much of his work was original and how much merely a repetition of the knowledge of his master is unknown. Strömberg (1937) states that Theophrastus had access to a rather comprehensive literature on the subject of botany, written before his time. In any event, although Theophrastus himself did some traveling, much of his compilation is based on the verbal reports of men who accompanied the army of conquest of Alexander the Great and of other travelers in the Near East and especially in Egypt. Hence much of his information must have been the common knowledge of the vinyardist, of the olive and date culturist, of the cultivator of fruits and grains, and of the rhizotomist or collector of roots and herbs for medicinal purposes. Amounting almost to folklore, much of this information must have gone back many hundreds of years before Theophrastus put them into writing.

Of the works of Theophrastus, we have today several manuscript copies of two sets of books, both generally believed to be complete: the earlier one, translated into English as "Enquiry into Plants" or as "History of Plants", consists of nine books; the later one, "Causes of Plants", of six books. For the present review the first nine have been seen in German and English translations (Sprengel, 1822; Hort, 1916), and the first book of the "Causes" in an English translation (Dengler, 1927). Information on Theophrastus has also been obtained from Sprengel

(1817), E. H. F. Meyer (1854–1857), Lenz (1859), Jessen (1864), Hoefer (1872), Kirchner (1874), Sachs-Garnsey-Balfour (1906), Hawks and Boulger (1928), Strömberg (1937) and Cohen and Drabkin (1948).

In the "Causes" Theophrastus stated that in both budding and grafting, the ingrafted part uses the other as an ordinary plant uses the ground; budding is really a kind of planting in which the germinating and supporting force is the vital moisture; the bud, having this moisture, is suited to the other part, and the part having the nourishment grows the bud as though it were its own; growth takes place readily because the nourishment is, as it were, predigested. Further on, Theophrastus said that "annual budding"—growth of twigs from the natural buds on the parent plant—is really a sort of second generation, thereby emphasizing the individuality of the twig; and again, "each of the shoots is, as it were, a plant in the tree instead of in the earth".

This theory of growth, which thus became established in Greek philosophy, lay dormant for many hundreds of years, like most other Greek knowledge. The Romans seem to have passed it by. It appeared again at the beginning of the eighteenth century when Hire (Lahire) (1708) elaborated upon it. Giving credit to "learned philosophers" for the idea, he added that each terminal and lateral bud contains an egg of the species of plant or tree on which it grows. When the egg germinates and grows, it produces a new individual plant of the same species, consisting of a stem which grows into the atmosphere, and a root which grows downward between the bark and wood, as can easily be seen, he says, by cutting into the stem; and in some South American trees it is readily observed that they penetrate the soil.—Was he perhaps thinking of closely appressed lianas?—By their lateral union, the bud-roots of a season form a new layer of wood.

Wolff (1759) believed that bundles grow down from leaves, the stem being a continuation of all united leaf stalks and composed of as many bundles as there are leaves; each leaf, he thought, contains a single bundle. Bundles growing downward from the leaves unite to form a solid cylinder of bundles in the stem. Every year a new additional set of bundles grows downward, each set forming a growth layer. Wolff was apparently unaware of previous literature on the subject.

The noted French botanist and forester, Duhamel du Monceau, considered (1764) that the eye of the bud, as gardeners call it, is a branch in miniature. Each cone of woody growth, he said in the Oelhafen translation (1764), is a separate and distinct tree which has grown over and beyond the similar tree formed during the preceding year.

Erasmus Darwin (1789, 1790, 1800, 1801), who did not state the source of his ideas, went a step farther in that he emphasized the origin of bark, as well as of wood, from bud-roots. A tree is, properly speaking, a family or swarm of buds, each bud being an individual plant, hence truly an annual plant.

On the other hand, the British botanist and horticulturist, Knight (1801), rejected the theory completely.

According to Agardh-Meyer (1831), a theory of bud-roots had been propounded by J. C. F. Meyer (probably 1808).

The most persistent advocate of the theory of descending roots from buds is the French botanist, Louis Marie Aubert Aubert Dupetit-Thouars, whose name is written quite variously in the literature. His theory was apparently first presented in 1805, and again in 1806, 1807, 1809, 1815, 1816 and 1819; of these papers the first and last have not been seen by us. His paper of 1807 has been completely reviewed by Schumann (1873). Dupetit-Thouars believed that a bud originates from a parenchymatous sap and represents a complete embryo; it sends out from its base fibers which grow very rapidly, even with the speed of electricity and light. Every such fiber finds in the mucilaginous moisture between bark and wood an excellent culture medium which stimulates rapid downward growth. Since several fibers grow downward simultaneously, they unite to form a bundle, and they are held together as a bundle in the stem and root. The natural tendency of the fibers to become dispersed and isolated, we are farther told, is not completely fulfilled until they reach the smaller roots, where each fiber becomes a distinct root hair. All buds behave similarly; they make a direct connection between the leaf and the root and grow downward in straight lines; by lateral union they add a new layer of wood to the twig, the branch and the trunk (and presumably to the root also). This can be easily proven by pulling off a bud downward on the stem. New buds are formed each year from the sap. Each of his successive papers adds more de-

tails. He apparently considered his theory to be original with him; yet in other connections, he referred to the works of Theophrastus and of Erasmus Darwin.

This French scientist had a considerable influence on the botanical thought of his day, and we find his version of the bud-root theory repeated, with modifications and additions, by a number of later botanists, even if they were not all convinced of the correctness of his details. According to Sprengel and to M. Agardh, a Prussian lawyer named G. F. Moeller (1751) had propounded a theory like that of Hire; and Linnaeus (Rose, 1775) entertained a similar idea. Willdenow-Link (1821) agreed in part, but asked for more experimentation and proof. Evelyn (1825) cited it briefly, as did Agardh-Meyer (1831). Candolle (1831) leaned toward it.

Poiteau (1831) strenuously called attention to the fact that, instead of being original, as Depetit-Thouars thought, the theory is merely a repetition of that of Hire (1708), whom he strongly defended and whose theory he further elaborated. Candolle (1833*a*, *b*) viewed a tree as being composed of as many individuals as there are parts derived from buds. Lindley (1833) held some parts of the theory to be questionable. Reum (1835) considered the root to be a separate and distinct individual. In a later work Link (1837) and Lankester (1840) mentioned the bud-root theory. Meyen (1839) considered a bud to be an individual plant, and Unger (1840) thought of buds and branches as individuals which live parasitically on the mother stem.

The careful work on the cambium by Mohl (1844) and others cast the bud-root theory into the discard in favor of the relation of growth to the physiologic activities of leaves, but there remained some adherents to the older idea until the middle of the nineteenth century (Candolle-Kingdon, 1839-1840; Gaudichaud, 1841, 1852; Theodor Hartig, 1853; Lindley, 1862).

One important phase of the theory, however, has refused to die: the idea of the individuality of buds and branches. Indeed, in a quite recent paper, Murneek (1939) considers that both structurally and physiologically a tree is a " colony " of more or less independent units, the branches.

Thus the idea of the individuality of branches has persisted from the fifth century B.C. to the twentieth, A.D.—a span of 2500 years!

TIP GROWTH FROM THEOPHRASTUS ONWARD

The most obvious aspect of growth, aside from that associated with germination of the seed, is the extension growth which takes place at the tip of each twig. This phenomenon received the attention of Theophrastus (Sprengel, 1822; Hort, 1916; Dengler, 1927; and others) who anticipated some of the more complex problems of growth in length.

Because of a term which has been translated as "budding", there has been some confusion in interpreting Theophrastus' meaning and even in understanding that he was dealing at all with the problem of growth in length. Aside from its use in connection with one type of grafting, the term was used by Theophrastus to mean the formation of a bud, the formation of a cushion below the bud, the opening of a bud, the growth of a bud into a twig, or two or three of these meanings together; and the term "bud" was sometimes used as the equivalent of twig (Sprengel, 1822). Our interest is in those passages in which it refers to the growth of a bud into a twig. There is also some confusion about the term translated as "loosening" or "peeling of the bark", by which Theophrastus seems to have meant that, at certain seasons of the year, man finds it easy to loosen or peel off the bark, not that it does so of its own accord, as it is actually translated. With these interpretations, much of what he wrote about tip growth sounds rather modern.

Opening of the buds and growth of the twigs, he tells us, begin in the spring at such time as the bark can be readily peeled off, that is, with the first sap flow. In Greece such extension growth usually ceases in a few months, whereas in Egypt it may continue for almost the entire calendar year. Trunk and branches grow in length during spring and summer until the leaves fall. Theophrastus believed that extension growth in roots occurs only during the winter months.

A definite season of length growth is further recognized in the statement that trees make their growth all at once or nearly so, whereas herbaceous plants may be seen to grow and flower at any and all seasons of the year.

Trees growing close together grow and increase more in height, and so become unbranched, straight and erect; while those that grow far apart are of greater bulk and denser habit, growing less

straight and with more branches. Reasons are not guessed at, nor are the applications to forestry touched upon.

Terminal bud scale scars and branch whorls are described but not recognized as annual. " The periods of budding can be seen in all trees, but especially in fir and silver-fir, because the joints of these are in a regular series and have the knots at even distances ".

Theophrastus managed to touch upon some very fundamental ideas: the relation of extension growth to the flow of sap and to the presence of leaves, the relation of length growth in the root to that in the stem and of tip growth to diameter growth, and the effect on growth of density of the stand. The influence of climate is also discussed at length. Some of these thoughts have persisted in the minds of botanists well into the nineteenth century, and some are considered today to be fundamentally accurate.

In the days of the Romans very little original work was done in botany. Pliny the Elder seems to have contributed nothing new on tip growth.

Fourteen hundred years later, Leonardo da Vinci (McMurrich, 1930; MacCurdy, 1938) made an unsuccessful effort to determine the age of a branch by its phyllotaxy.

We have been unable to determine who was the first to recognize the fact that in the North Temperate Zone a single tip flush is generally formed in the course of one year, and that its boundary can be determined by the presence of the scars of the terminal bud scales. As common knowledge among foresters and orchardists, the information is perhaps quite old in central and nothern Europe. By the middle of the last century it was quite generally recognized (Wigand, 1854; Schacht, 1860; etc.), although exceptions of several kinds were known even then.

Rees (1929) used the term " primary growth " for tip growth, and called diameter growth " secondary growth ". Various terms have been applied to the single annual tip flush, or to the first flush of several in the case of multiplicity, such as May shoot, spring shoot, summer shoot, first shoot, spring extension growth, and twig extension. A confusing element is introduced by use of the term " internode " for the distance between branches in conifers instead of the distance between leaf bases; in uninodal pines such an internode represents the terminal growth of a year, whereas in multinodal pines it corresponds to the growth of only

a part of the growing season. MacDougal (1939) suggests substituting the term " segment " for such an " internode ". Jacobs (1937) uses the expression " unit of length growth " for the shoot which is derived from a single bud, whether annual or intra-annual. Belief that in pines a single branch whorl is formed in one year goes back at least to Schober (1753).

Attempts were made by Areschoug (1875–1876, 1877) at classifying all types of branches. Pammel (1893) and others distinguished between definite annual growth, which stops when terminal buds are set in the summer, and the indefinite, which continues until stopped by cold weather.

The topic of length growth in roots is of interest because of the long-drawn-out argument, which began with Theophrastus (see above) and Duhamel (1760), as to whether they grow in length during the winter.

Bradley (1716) proposed a very unique theory to account for length growth in roots and stems: vapors are taken in by the roots, passed upwards in the vessels through root and stem to the extremities of the branches, where they meet parts resembling glands; the vapors at the tips of the branches come near the air, are condensed, and return downwards between the four bark layers by means of their own weight, leaving in each bark layer of both stem and root the juices which they need, till at last the more oily part, passing to the root, lengthens its fibers " as icicles are lengthened ". This is only one of many theories to account for the growth of stem and root, which involve refining of the sap.

GROWTH LAYERS AND THEIR ANNUAL CHARACTER

Details of diameter growth, because they are internal and take place on a smaller scale, are much less obvious than are those of growth in length. No written record of diameter growth has been found to antedate the writings of Theophrastus, and his understanding of the process was quite meager. It is true that he discussed the age of some well-known old trees, but their ages were estimated in part from their diameter and in part from " mythological beliefs ". Since many trees are said in his account to grow chiefly or only in the direction of their height, as the silver-fir, date palm and cypress, diameter growth is inferred in others. His knowledge of secondary growth in thickness has indeed, been vari-

ously interpreted. Uzielli (1869) stated that he knew nothing about tree rings; Greene (1909) claimed that he understood the manner of formation of the growth ring; and Green (1914) said that he was acquainted with annual rings and with secondary thickening. Nördlinger (1874) hypothecated that the Greeks were fully aware of the fact that one ring is formed in the stem each year, for they could not have helped but notice, when felling trees, that a thick trunk is made up of many rings and a thin one of but a few; nor could they have failed to guess the relation of rings to age during their abundant work in grafting with one-, two- and three-year-old wood. The truth about Theophrastus, however, lies in the middle ground between these extreme statements, unless the problem is discussed in those books of the "Causes" which we have not seen.

Four aspects of the question of growth layers concern us here. The first is recognition of growth rings as such, regardless of their time or method of formation; the second is their annual character; the third, their structure; the last, their origin.

That growth rings were seen by Theophrastus, there can be no doubt. Rings would seem to be referred to in his statement that round timbers (like those used for masts and yard-arms) have several cores, although his description of these cores leaves some doubt as to his actual meaning. Coniferous wood was probably the most common kind used for such purposes, and mention is frequently made of both Greek fir (*Abies cephalonica*) and silver fir (*A. pectinata*). The present distribution of silver-fir includes the mountains of Greece (Schacht, 1860; Gordon, 1880; Bretzl, 1903), as does also that of *Abies cephalonica* (Dallimore and Jackson, 1923). It is at least possible that the statement above concerning cores refers to the growth rings of these species.

There is, however, much more definite proof that Theophrastus recognized growth layers. We agree with Strömberg (1937) that Theophrastus did not always make a clear distinction between bark and wood, in so far as growth rings are concerned; nevertheless, it is clear to us that he recognized the presence of rings in both bark and wood in at least two species of conifers. In the translations of the "Enquiry" by Sprengel (1822) and by Hort (1916), we find a statement that the bark of the silver-fir has many layers, like an onion; there is always another layer beneath

that which is visible, and the bark is composed of such layers throughout. Sprengel added that the bark of this species does actually occur in layers. One could guess that Theophrastus might have had both bark and wood in mind, and this supposition receives support from a statement a few pages further on, where it is stated that in the Greek fir the arrangement of the rings in the heartwood is "bark-like". Neither bark rings nor wood rings are specifically mentioned in any other species than the fir and silver-fir, nor are these rings given an annual character. Neither did he mention them as intra-annual layers, that is, as multiple growth layers, two or more of which are formed in the course of a single growing season.

Several important questions arise from this discussion. Why were growth rings mentioned in only two tree species, and those species of conifers? Why were these rings not recognized as annual rings? Why were multiple rings and partial rings not mentioned? These problems have not been touched upon in the voluminous literature on growth layers, except for the suggestions made by Uzielli, Greene, Green and Nördlinger. The answer to some of these questions lies in the geographic location of Greece and in the fact that the foreign botanical connections of Theophrastus lay to the south and southeast of Greece, and not to the north.

It is a well-known fact that, in general, growth layers are most "regular" and "normal" and most sharply defined in the far north and on high mountains (Griggs, 1938; Hustich, 1948; Marr, 1948), and that they become progressively more irregular and more poorly defined toward the tropics, both wet and dry (Penhallow, 1885, 1907; Tschirch, 1889; Antevs, 1917). It is also well known that coniferous trees become progressively fewer as one goes from the north into the tropics, especially in Europe and Asia. Firs and pines belong predominantly in the Temperate Zone. Studies of tree rings do not seem to have been made in Greece since the time of Theophrastus, except for measurements of total diameters by Professor Schmidt on *Populus alba* (Pokorny, 1865–1866). In Anatolia in Asia Minor, however, Gassner and Christiansen-Weniger (1942) find conditions ideal for the study of multiple growth layers, and in Palestine Gindel (1944) and Oppenheimer (1945) find that the Aleppo pine forms

numerous multiple rings. It is a reasonable guess, therefore, that very many of the trees of Greece will be found to show multiple growth layers as well as numerous "irregularities" within these layers, such as lenses and half-lenses. As will be shown further along, Theophrastus found multiple tip flushes in abundance; and while multiple diameter flushes do not necessarily accompany multiple tip flushes, there is a good chance that they very often do, especially in dry tropical and semi-tropical countries. As will be shown later, Theophrastus' knowledge of multiple tip flushes was far in advance of his time, whereas his understanding of growth layers in the wood was decidedly deficient. Again, why?

Closer examination of the situation will bring to light some very interesting comparisons. By far the larger number of botanists who have studied tip and diameter growth in trees have lived and worked in the North Temperate Zone, in which second tip and diameter flushes are the exception rather than the rule, in which growth rings are usually clearly defined and annual in their formation, and in which coniferous trees are very abundant. The home of Theophrastus in Greece lay in a latitude perhaps 400 miles south of that of northern Italy, from which Leonardo da Vinci and later Montaigne reported well-defined annual growth layers; nearly 700 miles below the latitude of Paris; 1000 miles below that of London and Berlin; and still farther from those of Denmark, the Scandinavian countries and Finland, all of which represent later centers of studies in tree growth. Had Theophrastus lived in San Francisco, which has approximately the same latitude as Athens, his writings would have been concerned largely with that area, with Santa Barbara (corresponding to the Island of Crete) and with a large portion of northwestern Mexico (the equivalent in latitude with Memphis at the apex of the Nile delta). There is mention in Theophrastus of the flora of the mountains in Greece and Crete, which brought him into contact with some of the northern forms, especially with the fir and silver-fir; but he seems to have known very little of the world to his north and northwest. That unknown world, containing the centers of future research on tree growth, has the following rough latitudinal equivalents on the west coast of North America: Pisa in northern Italy with the California-Oregon boundary; Paris with the United States-Canadian boundary; London with the northern

end of Vancouver Island; Berlin with the middle of British Columbia; Oslo, Uppsala and Helsinki with the northern end of the Alaska panhandle. Indeed, Theophrastus almost lived in a world apart from the rest of Europe, not only geographically but in the sense of tree growth as well. Many plants of southern Europe, as the olive and the oleander, have very indistinct rings (Sanio, 1863; Müller, 1888; Dallimore and Jackson, 1923; a series of articles on the region of Bari, in southern Italy, beginning with Giannuoli, 1947). This must be even more true of Greece, Crete and Egypt.

It is little wonder, then, that Theophrastus mentioned growth rings in only two species, the Greek fir and the silver-fir, both of which are more northern coniferous trees found in Greece near the southern limit of their ranges, and there only in the higher mountains. One cannot agree with the suggestion made by Nördlinger (1874) that the Greeks must have known that growth rings are annual; indeed, we can safely infer that Theophrastus must have had such an abundance of multiple rings on hand that he did not recognize the annual character of any of the rings.

We have now answered the first two of our problems concerning growth layers. The third, dealing with their structure, is more difficult to solve. Theophrastus divided the stem into pith, wood and bark, as is still commonly done today. The grain of wood is mentioned on numerous pages, and this of course refers directly to ring and ray structure. He tells us that, as compared with trees growing close together, those growing far apart have harder wood and closer grain. In other cases grain and rings are inferred; thus the best timber came from Macedonia where it grew in the mountains—best, no doubt, because it was close-grained.

Recognition of growth rings implies recognition of early and late wood. The statement above on harder wood can mean nothing else than a larger proportion of late wood, and closer grain must mean thinner rings. That thin rings have a larger proportion of late wood has been abundantly proven by Schacht (1853) and others. Theophrastus also occasionally mentioned the density of wood, a closely related problem.

There is a large body of literature on the best season for felling trees. In the United States, where logs are stored in the water of

mill ponds, the problem seems not to concern us. But where freshly cut timber is stored on the ground before being sawed into lumber, there is often a real problem of rapid fungous decay. A recent very extensive work by Gäumann (1930) in Switzerland shows that timber cut in the spring when the sapwood is very wet will decay much more rapidly than that cut in autumn or winter after the drier late wood has been laid down.

This problem, too, seems to have begun with Theophrastus. Round timbers (for masts, etc.) should be cut in the spring when the tree is coming into leaf, for then the bark strips easily. Other trees, he says, especially those timbers which are for underground use, are cut in September or some time after the wheat harvest; among these, mention is made of oak, elm, maple, ash, beech and lime (*Tilia*). Oak is cut latest of all, in early winter or at the end of autumn; if it is cut at the time of peeling, it rots almost more quickly than at any other time, whether it has bark on it or not; this is especially so if it is cut during the first peeling, less so during the second, and least during the third. Again, wood is stronger if cut after ripening of the fruit.—It should be clear from these examples that Theophrastus had a fair concept of early and late wood, even though he nowhere directly discussed the parts of a growth ring.

The fourth problem of growth layers, that of their origin, is scarcely touched upon by Theophrastus who knew however, that growth takes place in both bark and wood. In some trees, he says, as cork oak, cherry and *Platanus,* new bark is said to form under the old bark which withers and cracks and may fall away of its own accord; there is no suggestion at all about the origin of the wood. The cambium layer is very dimly anticipated in his knowledge that the bark peels off easily when the tree is in sap, because there is a fluid under the bark. Many hundred years later this fluid itself was called the "cambium", was believed to give rise to the bark, and the latter in turn to the wood; these Renaissance ideas may easily have been derived directly from Theophrastus.

The later scientists of Greece and of Alexandria, Egypt, are said to have followed the botany of Theophrastus rather closely and to have developed little or nothing that was new.

Pliny the Elder (c. 23–79 A.D.) appears to have been the only Roman to write extensively on trees. Of his 37 books on natural

history, Books 12 to 21 treat of trees, plants and flowers. These have been studied in the Bostock and Riley translation (1855–1856). The comments of Stone (1921), Hawks and Boulger (1928), and of Ugrenović (1938) have also been seen.

Pliny lived in northern Italy much of his life and should therefore have been able to study a greater number of trees which are typical of the North Temperate Zone than was Theophrastus. But he was so busy compiling his 37 books on natural history from some 2000 different Roman and foreign writings that he had little time for original observation. What these writings were and what they may have contained on the growth of trees will forever remain a mystery, for Pliny seems not to have been much interested in the subject. He himself contributed very little new material other than a description of the very fancy types of grain in some very valuable tables whose large tops were made of citrus wood. He discussed the age of some old trees, but not from growth layers; trees from certain localities, such as the mountains, are of the highest quality—no reason is given; and early and late wood are noted in dicotyledonous wood, for they constitute light and dark zones. The bark of the cork tree is remarkably thick, and if removed it will grow again. Some of these statements are actually less detailed than the corresponding statements in Theophrastus.

The following very interesting statement is taken from Hawks and Boulger (1928): "When, about A.D. 850, the Caliph Motewekkil cut down all the sacred Cypresses of the Magians, this one is said to have shown 1450 annual rings of growth". Further details, which would be so interesting and illuminating, are lacking.

Growth layers are apparently not again mentioned in botanical literature until the thirteenth century. Albertus Magnus (?1193–1280), also known as Albert von Bollstädt, mentioned ring-like layers of wood in the alder (Hawks and Boulger, 1928); his concept of rings in general was not the same, however, as is ours today, for he seems to have considered the structures to be rings only if the rays are not so broad as to be seen with the unaided eye before the wood (E. H. F. Meyer, 1857).

Recognition of the annual character of growth rings in northern Italy by Leonardo da Vinci and later by Montaigne has been frequently noted (Glock, 1941). Leonardo (Uzielli, 1869; Toni,

1922; McMurrich, 1930; Baldacci, 1940) no doubt worked out the problem independently; Montaigne (Dédéyan, edition 1946) got his information from artisans who worked with wood. In both cases the knowledge came from northern Italy, where no doubt most of the trees used had been cut in the mountains, the alps and the Apennines, in which growth layers are known to be prominently bounded and to be largely annual in character. It would appear very likely, indeed, that the knowledge of the engineer, Leonardo, was passed on in his own time to the wood industry which, some 80 years later, transmitted it to Montaigne. Both Leonardo and Montaigne also dealt with the problem of eccentricity in the trunk.

With these two writers and the knowledge harbored by Italian artisans, the annual character of growth rings in trees should have become well established in the minds of botanists; but such is not the case. The post-Renaissance botanist was a taxonomist who looked down his nose at things anatomical. Furthermore, Leonardo's botanical writings remained unknown until less than a century ago, and Montaigne's reference to growth rings was discovered by botanists only a short time before that. And again, the layman's knowledge is all too often ignored by the scientist. It was, therefore, necessary to rediscover the fact that growth rings in the wood are annual in character.

Credit for this rediscovery is generally given to the plant anatomists Malpighi (Möbius, 1675, 1679) and Grew (1682). Malpighi's work marked the third time for this discovery in Italy. These two botanists, mainly interested in the anatomy of individual cells, contributed very little to their organization into growth rings, in so far as found in the books available to me.

At about the same time there appeared some first class completely forgotten work on "tree rings" by the Dutch microscopist Anton van Leeuwenhoek; exact dates have not yet been checked, and hence priority not established between Malpighi, Grew and Leeuwenhoek. It is unfortunate that the latter has of recent years been pictured merely as a hunter of curious odds and ends, for this does grave injustice to some of his work, especially that on plant anatomy (compare the estimates of Sachs, 1906, and Jessen, 1864). The details and accuracy of his beautiful drawings of cross sections of wood, made by a professional artist, as reprinted

in Hoole (1816), would do credit to a modern textbook in plant anatomy. Their written descriptions, also excellent, repeat several times that each circle in the wood of a tree undoubtedly marks the increase in growth of a single year.

Doubts of the annual character of rings, which persisted in central Europe, were partially laid at rest by Schober (1753) who showed that in a pine tree known to be 22 years old, the number of rings agreed with the number of branch whorls at the 5th, 10th, 15th and 20th whorls. He admitted, however, that he had seen a few thin rings in the Carpathians which may not have been annual, and he suggested that further proof of the annual character of rings could be obtained by counting the number of rings formed, since certain " monuments " (inscriptions?) had been left on trees by hunters.

According to Goeppert (1868), who did not mention Schober, a number of people, beginning about the middle of the seventeenth century, were able to prove the annual character of growth rings by the study of " monuments " and dated inscriptions in trees; the number of years which had elapsed since the inscription was cut corresponds with the number of growth layers which had overgrown the inscription.

Soon, however, the annual character of rings became very widely accepted in Europe, as is attested by the works of Linnaeus (Holmboe, 1910), Duhamel du Monceau (Oelhafen, translation 1764), Winterfeld (1791), Medicus (1799), Kieser (1812), Willdenow-Link (1821), Evelyn (1825), Candolle (1827, 1831), Agardh-Meyer (1831), Reum (1835), Dutrochet (1837), Link (1837) and Meyen (1837). Of these, we find some reservations or doubts only in Winterfeld, Evelyn and Agardh-Meyer. All of this seems to have established firmly the principle that the age of a tree can be determined by the simple process of counting its rings.

ANATOMY AND CLASSIFICATION OF GROWTH LAYERS

Two adjacent growth layers, in order to be recognized, must be separated by a distinguishable boundary between them. In the Temperate Zone this usually becomes a matter of establishing the differences between early and late wood, or differences in the distribution or size of vessels. In simpler cases this is so obvious

that it was evident to the Greeks, the Romans, to Leonardo da Vinci, Montaigne, Malpighi, Grew and Leeuwenhoek, as previously stated.

Leeuwenhoek (Hoole, 1816) gave excellent written descriptions and detailed figures, as seen with his microscopes, of the growth rings of fir, oak, elm, beech, willow and alder, describing accurately the differences between the wood laid down during spring and that toward autumn. A piece of ebony wood from Mauritius is described as being without rings because it grew in a tropical climate. Rings are also absent, he wrote, from boxwood; no explanation is offered. His breadth of view is shown by the fact that he selected representatives of conifers, ring-porous species, diffuse-porous trees and trees in which boundaries are absent. Although no terms are applied to the ring types involved, each type is clearly and accurately described and depicted, and its late wood distinguished from the early.

It is surprising that such a clear understanding of the two major parts of a growth layer were followed by a marked deterioration in the knowledge of growth layer anatomy. John Hill (1770), who had at his disposal a good compound microscope, shows several drawings of cross sections of branches of English trees from pith to bark, with considerable detail of structure. But —a fact which does not seem to have been noted in the literature —he has some of his rings backwards, the outermost part of some of the layers containing the larger and more numerous vessels! Medicus (1799) was not certain of the cause but thought that the shaded appearance in the outer portion of a ring might have indicated denser tissue caused by thicker fibers. Microscopes were apparently not yet in general use. Kieser (1812), who must have had a microscope of some sort, did better, for he tells us that the larger vessels in a ring occur nearer the pith and are formed in the spring; the smaller ones are formed in autumn and occur in that part of the ring nearer the bark; this is correctly shown in several of his figures, but his Fig. 86, a cross section of the stem of *Rhus typhina,* is apparently copied from Hill and shows the reverse position of early and late wood.

Beginning with Evelyn (1825), rings are generally described with accuracy and the relation of the parts reasonably well understood. Agardh-Meyer (1831) tells us that some writers

(Sprengel, Dutrochet, Candolle) add a third layer to the typical early and late wood, a layer composed of thin-walled cells which bounds every ring on the inside.

The two major parts of a ring, at first merely described and not named, were soon called "spring" and "autumn wood", it being generally believed that the cambium remains active well into the autumn and even into the winter. And when it became known that the late wood is formed during summer, we find the older term retained for many decades (Schacht, 1853; Haberlandt, 1884; Wiesner, 1898; Benecke and Jost, 1923; and wood technologists in general). The term "summer wood", however, gained slowly in favor.

A new concept entered the picture when R. Hartig (1888) divided the ring of a coniferous tree into three zones: a spring zone, laid down in April and May, a summer zone of May and June, and an autumn zone; sharp boundaries between these are not always present, any more than between the older spring and autumn woods. The intermediate layer was accepted by Strasburger (1891) who gave it the name "Folgeholz" (ensuing or subsequent wood). Janssonius (1906–1908) used the terms "early wood", "middle layer" and "late wood". The terms "early" and "late wood" are used today for the two commonly recognized parts of the growth layer, in both coniferous and broad-leaved trees; these time terms have an advantage over "spring" and "summer wood" which are also time terms, in that they are properly applicable to the parts of multiple rings. The purely anatomical designations "light wood" and "dense wood" have been suggested.

Under unusual conditions a ring may be composed of a single part. Schacht (1856) showed that in wet moor soils *Pinus silvestris* forms only spring wood in its broad rings. When ring boundaries are absent, as in many of the trees of the tropics, only spring wood cells may be formed. It often happens, after insect or frost injury, that a growth layer may contain only late wood, the early wood being wholly absent. Lenses are often found to contain only late wood at their cusps.

Several botanists have been led astray by the primary xylem. Since a clear distinction was not made between the meristematic cells near the tip of the stem (cambium ring) and those in the

true cambium until about a hundred years ago, there could of course be no distinction between the primary and secondary xylem. The primary xylem was recognized as a distinct region by John Hill (1770) who called it the "corona". This zone was believed by Hill, Link (1807), Hundeshagen (1829) and again Link (1837) to be a ring of bundles laid down somehow after the first true ring has been formed, between the latter and the pith.

The presence of reaction (compression) wood within a growth ring does not often cause confusion, but there have been instances in which it was mistaken for late wood.

A variety of methods of classifying the growth layers of "normal" Temperate Zone trees has been proposed. The oldest is a division into those of gymnospermous trees (without vessels, in our modern sense) and broad-leaved or dicotyledonous trees (with vessels). This seems to hold in all but two instances: (*a*) vessels are present in the advanced gymnospermous order Gnetales, containing the three genera *Ephedra, Gnetum* and *Welwitschia*; (*b*) a few primitive dicotyledonous families, e.g., the Winteraceae (I. W. Bailey, 1944), are completely without vessels. The dicotyledonous group has been very commonly further subdivided into ring-porous and diffuse-porous species, depending on the distribution of the vessels; in the Temperate Zone these two subdivisions are rather sharply separated, one from the other, while in the tropics there are many intermediate conditions. Janssonius (1906–1908) found several tropical trees to show vessels mainly in the middle of the growth ring, whereas in others the middle had the fewest vessels. Chowdhury (1939*b*) also reports that a zone of vessels may be present only in the middle of the diameter increment.

Tiemann (1942) prefers very simple terminology for the two broad-leaved groups: woods in which pores vary in size from early to late wood, and woods in which pores are uniform in size throughout the ring.

There are very many more diffuse-porous species than there are ring-porous, even in the North Temperate Zone. Jeffrey (1917) considered the ring-porous condition to be uncommon at high latitudes and rare in the tropics, and Chowdhury (1939 *a*) states that nearly all dicotyledonous trees of India are diffuse-porous. The significance and the geographic distribution of ring-

porous and of diffuse-porous species was further discussed by Simon (1902), Antevs (1917), B. Huber (1935), and by Ladefoged (1952).

The cause of the differences between ring-porous and diffuse-porous woods has from time to time been sought in climatic or soil factors, operating either directly or indirectly; these are of course not true causes but, instead, influencing factors. According to B. Huber (1935), ring-porous woods have a biological advantage over diffuse-porous species, and the former are more plentiful in drier habitats. Simon (1902), working in the tropics, believed that the ring-porous condition is associated with the sudden development of leaves in spring. B. Huber (1935) shows that in ring-porous woods the transpiration current moves upwards about ten times as rapidly as in diffuse-porous species. This is true in spite of the fact that in ring-porous wood the water passes upwards only in the latest-formed growth ring (Rumbold, 1920; B. Huber, 1935), whereas in diffuse-porous species several rings of the sapwood are involved in upward conduction (B. Huber, 1935). Huber relates this apparent anomaly with the greater diameter and greater length of the vessels in ring-porous species.

Very important work on the growth of trees in the spring has been done by the "strip" method (Priestley, Scott and Malins, 1933). As the cambium swells in the spring, the bark slips easily over the wood, and a separation takes place in the plane of the cambium. For a time, all or nearly all of the new cells derived from the cambium are formed on its inner face; hence, when the bark is peeled off in this stage, the newly formed tissue is left as a soft layer overlying the lignified wood of the previous season. This can then be scraped off in long strips by means of a small knife or a screwdriver. The strips can be floated out in water and are very suitable objects for microscopic study. The cells are so plastic that they seem little injured, cytoplasmic streaming having been observed in some water mounts. The method is less effective after enough radial growth has occurred to make the strips too thick for examination; however, they can then still be obtained for a time by scraping the inside of the bark. The strips can be examined under the microscope either in water mounts or as fixed, stained and permanently mounted slides. By 1933 the strip

method had been used successfully on some 30 species of hardwoods and six of softwoods. It is again described in later papers (Priestley, 1935; Priestley, Scott and Malins, 1935; Priestley and Scott, 1938).

The method is much more rapid than any previously known for the study of the cambial activity of trees. A good deal of previous work has been corroborated with its use, especially on the time of beginning of cambial activity, on its basal progression (R. Hartig, 1894*a*) and on the length of individual vessels. Cambial activity begins much earlier in ring-porous than in diffuse-porous trees; it also progresses downwards from the buds to the roots much more rapidly, and the individual vessels are very much longer than in the diffuse-porous species.

A correlation has been attempted between the type of porosity and the evergreen habit in dicotyledonous trees. Simon (1902) found that in the evergreen species of the tropics the conducting tissues are rather evenly distributed throughout the growth ring and that they function for a long time; in deciduous species, on the other hand, conducting tissue is composed of larger cells chiefly in the spring wood, and their functional period is shorter. Working in India, Chowdhury (1939*a*), however, detected no correlation between the sharpness of the growth ring boundary and the evergreen habit, nor (1939*b*) between the evergreen habit and the presence or absence of growth ring boundaries. B. Huber (1935), working in central Europe, states that deciduous oaks are ring-porous whereas evergreen species of the genus are diffuse-porous.

The various facts here mentioned have led to speculation as to the significance of the ring-porous condition. The work of B. Huber (1935) emphasizes the highly specialized character of the pore zone in ring-porous woods. Chalk (1937) goes a step further and suggests that the ring-porous condition is completely distinct from and in no way related to the diffuse-porous condition; his point of view is that (*a*) the late or summer wood of ring-porous species is the equivalent of the entire ring of diffuse-porous species, (*b*) the pore zone in ring-porous trees represents an additional highly specialized tissue which has no equivalent in diffuse-porous woods, and (*c*) the term "early wood" should imply early development in relation to the foliage rather than to its posi-

tion in the growth ring and should be limited to softwoods (conifers) and to ring-porous hardwoods. In a later paper, Chalk (1937), after stating that for practical purposes it is often sufficient to speak of the inner and outer parts of a ring, suggests the following equivalents:

Conifers	Ring-porous species	Diffuse-porous species
	pore zone	
early wood	"early" wood	
late wood	"late" wood	
		entire ring
		(1) inner part
		(2) outer part

There has been some speculation on the origin of ring-porosity. B. Huber (1935) considers that the diffuse-porous condition is the older and that the ring-porous arose from it by an increase in the diameter of the vessels. The same conclusion has been reached in part by Gilbert (1940) from a study of the first growth ring of the stem, of the rings of seedlings, and of the "reversion" from the ring-porous to the diffuse-porous condition following wounding of the adult wood of *Quercus*. He considers ring-porosity to be more advanced from an evolutionary point of view; it has developed from diffuse-porosity as a response to climatic conditions characteristic of the North Temperate Zone. Chowdhury (1953) discussed the role of initial parenchyma in the transformations of diffuse-porous to ring-porous structures.

A complete classification of the types of growth layers has been only rarely attempted. One such effort is that of Geiger (1915) for teak in Java: (*a*) entire, "closed" annual rings; (*b*) partial, closed "annual" rings; and (*c*) intermediate [intra-annual] rings, which in turn may be entire and closed, partial and closed, or merely color rings [late wood layers of darker color].

In work with growth layers it is often necessary to know when the cambium begins its activity and when such activity ceases. A variety of methods has been devised for making such determinations, including diameter measurements with steel calipers, circumference measurements with steel tapes, increment borers, circumference measurements with various types of dendrometers, and dendrographs, and the "strip" method; summaries of methods are found in Antevs (1917), Büsgen-Münch-Thomson (1929) and MacDougal (1938). The recording of measurements

of circumference, diameter, or of the thickness of individual rings began, it appears, in the middle of the eighteenth century. Duhamel (1758) used a fine brass wire and also a fine copper wire for the measurements of the circumference of various trees, even going so far as to show that expansion and contraction of the wire with changes of temperature were too small to affect his results. Other early recorders were Marsham (1759), Winterfeld (1791), South (1792), Reventlow (preceding 1828, published 1934), Candolle (1831) and Hall (1839).

The most commonly used methods, however, of studying the details of cambial activity involve microscopic examination of a bit of tissue including the cambium, which may be obtained in any one of various ways. Interpretation always depends upon the number of rows of new cells formed and on a set of anatomical characteristics of the cambium region and of the tissues recently formed by the cambium. The most frequently used criteria are the radial dimensions of cambial and derivative cells, thickness of the cell walls, and the amount of lignification in these walls (Lodewick, 1928; MacDougal, 1938; and many others).

Wight (1933) feels that these criteria are not satisfactory; he proposes and uses in a study of cambial activity of *Pinus sylvestris* a complicated set of criteria which may be summarized as follows:

a) When the cambium is at complete rest, its radial walls are thick, its tangential walls have a uniform thickness, and the entire cambial zone is narrow and has a geometrical and almost solid appearance.

b) When the cambium begins activity, the cells of the cambial zone swell up and some of them differentiate directly without previous cell division.

c) When the cambium is in a stage of active cell division, there is a loss of regularity in the cambial zone, the radial walls of the cambial cells are still thick while its tangential walls are thin, and soon there is a smooth transition from the narrow cambial elements to the newly completed and completely differentiated tracheids.

d) When the cambium ceases to divide, the cambial zone again becomes narrow; next to it will occur a row of cells showing only little radial expansion; and next inward a zone of only partially

differentiated, somewhat thick-walled tracheids. Lignification is slowed down, the outer tangential wall being the last to lignify.

e) When a second period of diameter growth begins before lignification is complete, the situation can be recognized by the fact that lignification commences at once in the freshly formed tracheids.

Such a complete set of criteria for determining cambial activity has not been worked out for other trees. Details will certainly be found to differ somewhat from species to species, especially in the broad-leaved trees as compared with *Pinus sylvestris*.

MULTIPLICITY IN TIP GROWTH

It has long been considered " normal " for a tree, shrub or herb to make its total growth in length for a year in a single spurt which shows the typical sigmoid curve of growth; the single resulting tip flush reaches maximum length without intervening rest periods, and when it has completed its extension growth, a long rest period follows which lasts until the beginning of the growing season of the ensuing year. Such does in fact commonly take place in the North Temperate Zone, where most of the studies on tree growth have been made. But it is not the universal rule even there, for various trees, or individual twigs on a given tree, may show two or more periods of extension growth in a single year, alternating with more or less well-defined periods of growth inactivity.

The history of our knowledge of such multiple or intraseasonal tip flushes, like that of so many of our botanical problems, goes back to the Greeks. Theophrastus considered multiple tip flushes exceptional in Greece, for he wrote (Hort, 1916): " Now most trees, when they have once begun to bud, make their budding and their growth continuously . . .". Nevertheless, he devoted so much more space to multiplicity of tip growth that one wonders whether such phenomena were not so well known in his day as almost to amount to folklore. Continuing the interrupted quotation above: ". . . but with fir, silver-fir, and oak there are intervals. They make three fresh starts in growth and produce three separate sets of buds ". At least in the oak, these periods occur in May, June and July. On rare occasions there is in some trees a fourth growth from buds in September; such is more common

on the Island of Crete. And in Egypt there may be no cessation at all of twig growth, or the process may be suspended for only a short time.

The trees involved in the account of Theophrastus are both native and cultivated, both coniferous and broad-leaved. He described the supplementary flushes as being of two kinds, end-on-end from terminal buds (up to four in a series), and lateral growths from lateral buds. Mention is also made of second, third and fourth flowering and fruiting periods.

In dealing with the factors or causes of such multiplicity, Theophrastus was of necessity rather vague. The time of beginning of each tip growth is always associated with an increased sap flow, of which there are three or four, and with a period of easy peeling of the bark. Sprengel (1817) wrote of an old Greek maxim to the effect that the sap rises and the bark can be peeled three times a year. Theophrastus called the growth of a bud a sort of birth, and spoke of the phenomenon of additional growing periods as super-budding and super-germination; this was, of course, in line with his idea of bud-roots, previously discussed.

The two supplementary growth periods of summer are associated by him with the second and third sap flows, hence with a greater amount of moisture in the plant at those times. That of September is related to a healthy, vigorous plant, a good soil, and a long autumn with favorable growing weather and mild air. Still another recognized cause is defoliation: an olive tree, whose young shoots had been eaten off by locusts, grew again.

All in all, Theophrastus touched upon almost all modern aspects of multiple tip growth; even the background for their relation to hormones was very dimly anticipated; for, he says, if one permits the buds to remain on trees, the latter grow rapidly in length, but if they are removed early, the trees become shorter and more compact.

Multiple tip flushes were passed by completely by Pliny, except for mention of second and third flowering and fruiting periods in a single year in some orchard trees.

After the Romans the problem of multiplicity in tip growth was not again considered scientifically for hundreds of years. Simple observations must have been numerous on both second tip flushes and second periods of flowering and fruiting. For in-

stance, Kobel (1931) says that second tip flushes have been known in fruit trees since olden times. Scientific study of these phenomena, however, seems to have begun again with Duhamel (1758), Borkhausen (1800), Saussure (Vaucher, 1822) and Sénébier (8, i.e., 1800). Burgsdorf (1783–1800) considered second tip flushes normal and common in the oak.

During those early years, when meristematic tissues were unknown, all growth was attributed directly to the sap. The terms "May sap" and "spring sap" became almost synonymous with the first tip flush, and "August sap" with the second. In Germany the second flush is commonly called "Johannistrieb" (St. John's shoot) because of its unusual time of formation; in England, "Lammas shoot" for the same reason; in France, "l'été de Saint-Martin" and "sève d'août". Other terminology which has been used is "second bud", "August bud", "repeated formation of buds", "August sap", "autumn sap", "second shoot", "summer shoot", "repetition of shoots", "second sprouting", "repeated sprouting", "anomalous sprouting", "midsummer growth", "late-season growth", "secondary growth", "secondary elongation", "secondary elongation growth", "midsummer secondary elongation", "post-seasonal growth" and "secondary leafage"; and for the first and second shoots combined, "double shoot" and "double header". There are also many papers on the topic of "summer rest". The very fact that such a multitude of terms has been used is in itself proof that the phenomenon is anything but rare.

The types of second tip flushes were classified by Areschoug (1875–1876), by Ratzeburg (1868) and by Späth (1912); the latter (1912, 1913) has given us the nearest complete discussion in the literature of second tip flushes.

During the nineteenth century second tip flushes were discussed very extensively in Germany, Switzerland, France, England and Sweden, and in the twentieth century the United States and many other countries were added to the expanding list. Phases of the problem considered are mere recognition, abundance, species involved, the many types of tip flushes and their description, time of formation, number per year, influencing factors and causes, and artificial induction and suppression. The topic is indeed too huge to be summarized here in all of its phases.

Various factors and causes have been associated with the formation of second tip flushes. Many types of external factors have been invoked (Duhamel, 1758; A. Fischer, 1891). Unusual weather conditions are cited by Vaucher (1822), Nördlinger (1874) and Areschoug (1875–1876). Perhaps the most common of the external factors considered is temporary summer drought (Theophrastus; Agardh, 1832; Döbner, 1865; Schumann, 1873; Magnus, 1874; Nördlinger, 1874; Ward, 1892). Strong light is mentioned by Döbner (1865) and by Lakon (1915); defoliation by insects during the spring is proven responsible for substitution flushes by Döbner (1865), Ratzeburg (1868), Nördlinger (1874), R. Hartig (1892*a*) and many others; injury by rodents, by Ratzeburg (1868); damage by frost, by a host of workers; defoliation by storms, by Schrenk (1898). In nearly all cases the relation to newly formed leaves was noted.

It may be added parenthetically that the word "climate" is very often misused. Correctly applied, it of course means a composite or generalization of weather conditions throughout the year, averaged over a series of years. The term is altogether too often made to substitute for the state of the atmosphere at a given time, which is of course weather. Second tip flushes have been associated with both climate and weather.

An almost equal number of internal factors has been held responsible for second tip flushes (J. Huber, 1898), the oldest of which is renewal of sap flow by Burgsdorf (1783), Borkhausen (1800), Senft (1857) and Döbner (1865). The food accumulated and stored in late summer and autumn is largely used up by the growth of spring; accumulation of new food during spring was considered responsible for the second tip flush by Roemer (1806), Th. Hartig (1837*b*), Schacht (1860) and R. Hartig (1891). Earlier the "physiological action" of mature leaves was invoked by Hartig and Hartig (1836). And premature opening of the first set of buds was named by Candolle (1832). Increased water content in the tissues was considered by Hundeshagen (1829) and by Willdenow-Link (1821). Hundeshagen (1829) further considered the stimulating action of sap flow as a possibility.

It is of considerable interest that, long before heredity was at all understood, the capacity to form second tip flushes was regarded as inherent by Saussure (Vaucher, 1822), Sénébier (8, i.e.,

1800), Sprengel (1802), Candolle (1833*a*), Areschoug (1875–1876), Jost (1892) and Ward (1892).

The literature since 1900 for the most part follows the same pattern. The topic is well summarized in Büsgen-Münch-Thomson (1929), in other editions of Büsgen's excellent book on the growth of trees, and in Antevs (1917).

An interesting sidelight on heredity has been developed by comparison of second tip flushes with the growth of tropical trees. Magnus (1913) suggests that the central European beech and oaks develop second tip flushes because to do so is a matter of inheritance from evergreen ancestors, the periodicity of which did not coincide with the present European climate; the present beech and oaks have not yet adjusted themselves to the change in climate. Büsgen (1917) considers this possible but adds that the trees are nevertheless subject to modifications by external factors. J. Huber (1898), working with the periodic phenomena of the rubber tree (*Hevea brasiliensis*) considered the possibility that, in its original home, this species had adapted itself to several rainy seasons each year, and that this tendency has continued in its new home in the Hylaea in Brazil.

MacDougal (1938) suggests that second tip flushes will probably be found to depend upon the factors affecting the formation or disintegration of growth-promoting substances. The relation of growth hormones to second tip flushes is apparently an open field for research.

MULTIPLICITY IN DIAMETER GROWTH

Two thousand years were to pass between the time that growth rings in trees were first mentioned by Theophrastus and general acceptance by botanists of their annual character. The works of Leonardo da Vinci, Montaigne and Albertus Magnus were not known to botanists until the nineteenth century and consequently exerted no influence on botanical thought. Plant anatomy had its beginning as a science with the work of Malpighi, Grew and Leeuwenhoek in the latter part of the seventeenth and the early eighteenth centuries, and it was these three men who succeeded in establishing among botanists the fact that a single growth ring is formed each year. To them, then, goes the doubtful honor of establishing firmly the truth of that which is not necessarily true.

It must have been quite disconcerting to the botanist to dis-

cover that growth rings are not always annual, that indeed two or more layers may be formed during a single growing season. It has been shown in a previous section that Theophrastus must have come face to face with the problem of multiplicity of growth rings without recognizing it at all. Pliny and Albertus Magnus seem to have been ignorant of it. It must have been questioned before the days of the three plant anatomists mentioned above. And there were always some doubting Thomases, particularly in France, England and Germany. Perhaps the first clear statement of multiplicity appears in the writing of Duhamel (1758) who observed in France that trees known to be 20 years old did not always have 20 rings; that trees ten years of age sometimes had more than ten rings. This bombshell (for Duhamel was widely read, both in French and in translation) must have had its influence on a number of botanists, for we soon find recognition of multiple growth rings by John Hill (1770), Mirbel (1802), Sprengel (1802), Cotta (1806), Link (1807), J. J. P. Moldenhawer (1812), J. E. Smith (1814), Willdenow-Link (1821), Candolle (1833*a*, *b*), Reum (1835), Treviranus (1835), Bischoff (1836), Nördlinger and Poirson (1845) and a large number of other botanists to the present day.

Such heresy could not be accepted without strenuous opposition, especially in Germany where the science of forestry was developing rapidly. Burgsdorf, although describing the second tip flush of beech (1783) and considering second tip flushes both normal and very common in oak (1787), nevertheless stoutly denied even the possibility of the existence of second diameter flushes. The age of a tree can be definitely determined, he wrote (1788), by counting the number of wood rings: "This truth can be questioned only by simple-minded people who have no fundamental knowledge". Meyen (1837) stated that multiple rings are not possible, except perhaps in certain wet tropical regions with two harvests, summer and winter; they are not at all possible in most tropical regions. Theodor Hartig, who (1837*b*) had stated that the second growth ring might easily be mistaken for an annual ring, later (1860) doubted the existence of double rings; he had seen no cases of what looked like doubles to the unaided eye which a simple handlens could not refute. Wiesner (1890) claimed that all growth rings in Germany are sharp and distinct.

And in this country, the German-trained Fernow (1887, 1888, 1897), while begrudgingly admitting some difficulties in the determination of annual rings, was firmly convinced that the annual boundary can always be recognized; that the finding of multiple rings, common in the United States at that time, was in part merely a prejudice against the accepted theory, or a love of new discoveries, or a lack of sharp observation.—The letter of the law must be upheld at any cost!

Statements on the abundance of multiple rings vary widely, even when their presence is recognized. On the one extreme are the beliefs that they are very rare, occur in Europe in only a few species, and are always readily distinguishable from true annual growth rings. On the other extreme, John Hill (1770) was convinced that it is normal for two growth layers to be formed each year in all trees of England, one in spring, the other soon after midsummer. And Bechstein (1821) believed that double rings are found in nearly all German species of woody plants. Their presence in conifers was long denied, later abundantly substantiated. All of this refers to their "natural" occurrence; their formation after severe injuries, such as defoliation by insects, is accepted by all workers in the field.

Methods of studying multiplicity are several and varied. A simple observation that a branch on a tree has grown to a certain length during a season, and then examining cross sections at the base of the branch, is of questionable accuracy, even though often correct. R. Hartig (1869) thought he had a fool-proof method, one already used by Schober (1753), when he compared the number of rings at different elevations of young trees of *Pinus strobus* with the number of branch whorls, since up to that time it was not questioned that a single branch whorl is formed each year. In more recent times, however, many workers have shown that a number of species of pine may develop two whorls of branches in a single growing season. The same objection holds for comparing growth layers with the counts of terminal bud scale scars, for, as already shown, tip flushes are often multiple.

A method which has been used very extensively in older tree trunks is to follow a questionable ring completely around the circumference. This procedure will no doubt eliminate some double rings, but is by no means perfect.

Aside from the use of internal markers, to be discussed later, only one accurate method is known to us: placing definite marks at known points along a branch with a nail, notch, string or paint, and measuring the branches at the end of the growing season or at intervals. Thus Kny (1879), who wrote the first comprehensive paper on double rings, stressed the necessity of studying branches of known age. And Schrenk (1898) stated that ". . . in determining the age only a personal knowledge of the twig is to be considered".

Many terms have been applied to the rings of a multiple series, the most common being "double rings" or the anomalous term "double annual ring" for a series of two, and "false ring" or "false annual ring" for the second of such a series. The word "double" is also used for the outer ring of a pair, in the same sense as the double of a double rainbow. Among the many terms which have been gleaned from a large body of literature for multiple rings, we may mention the following:

summer ring
summer layer
accessory layer
summer follow-ring
St. John's ring
spring wood in the autumn wood zone
false early wood
fictitious ring
spurious ring
false ring
extra ring
superfluous ring
supernumerary ring
non-annual ring
quasi-circle
double rings
the double ring or simply the double
duplicate rings
triplicate rings
additional ring
second circle
doubling of vessels
repetition of vessels
half ring
half-annual ring
divided ring
secondary ring
secondary zone
sub-ring
intermediate ring
intermediate layer
intermediary ring
interrupted circle
ring appendage
midgrowth layer
frost ring
wound ring
moon ring (term with several meanings)
doublets
triplets

The process of doubling has also been called "duplicity".

Attention may here be called to the use of several confusing terms in connection with growth layers in general. The designation "ring" may mean a diameter increment for an entire period of growth as seen in cross section, that is, all of the wood laid down by the cambium during such a period; or it may mean such an increment even when it does not go completely around the circumference, as in a lens. Or again, it may mean merely the outer boundary of such an increment. Often the term is used in several senses in the same article. When a ring is described as being "absent", it may mean that there was no increment at all for the given period, the cambium having remained dormant, as may be the case at the base of the trunk in badly suppressed trees or in limbs and trunk after complete defoliation by insects; perhaps the best term for such cases is "omitted rings". Or again, "ring absent" may mean that the cambium failed to become dormant at all, so that the wood was laid down without interruption for two or more years; in this case it is not the ring which is absent, but merely the boundary. Such cases are well known in many tropical trees, in cacti and in certain other plants.

Since double rings do exist, and since they often resemble single annual rings (see below), there arises the question of the accuracy of ring counts in determining the age of a branch or trunk. This was, of course, doubted by all who did not recognize growth rings as annuals. For those who considered multiple rings as rareties, their relation to age was of little significance; for others they assumed a much greater importance, even threatening the very foundations upon which rests the science of forestry (Fernow, 1887, 1888).

Duhamel (1758), cited above, was probably the first to give reasonably accurate evidence that ring counts do not necessarily agree with age. This followed by a half century or more the "proof" by Malpighi, Grew and Leeuwenhoek that they do agree. Winterfeld (1791) also was not convinced, for he doubted that a large number of rings in an oak proves great age in the tree. Doubts were entertained by Cotta (1806) who nevertheless considered ring counts to be the most accurate method of age determination known.

The problem of age is not yet settled. While workers in all fields—botany, forestry, archaeology—recognize the presence of

false rings, there are some who believe in the absolute accuracy of ring counts as indicators of age; others are certain that errors are bound to occur. It is, of course, not a question of the mere presence of multiple rings, but, instead, one of whether they can always be recognized as such.

A large part of the confusion on multiple growth layers arises from their variable anatomy, and this depends in part on the time of their formation (Späth, 1912). If they arise from a cambium which has been rejuvenated after complete rest during summer, the second ring shows the same anatomy as the first, and neither can be distinguished from a normal annual growth layer. Over a century ago, Unger (1847) reported five conditions in the outer boundaries of the first and second rings: that of the inner ring less sharp than that of the outer, which is the most common situation; the boundaries of both rings sharp in *Sambucus*; that of the inner sharper than that of the outer in *Robinia*; in the case of three growth layers in *Salix* and *Alnus*, the outer boundary of the inner ring sharper than those of either of the two intra-annuals; and finally, neither boundary sharp in *Corylus, Robinia, Populus* and *Salix*. And Jost (1893) found three types of outer boundaries on the inner ring—distinct, indistinct and none; the type of boundary depends on the stage of the late wood in the first ring at the time the second ring begins to be formed. Jost's last type of boundary creates what Glock (1951) has called an "invisible ring". Treviranus (1835) stated that the second ring is formed only if there is a break in the growing period; many others have agreed. If, on the other hand, rejuvenation takes place before the cambium has reached a complete rest (has merely slowed down in its activity), the boundary between the first and second growth layers will not be sharp; and the sharpness increases in proportion to the degree of slowing down. Jost (1891, 1893) alleged that the presence of double growth rings depends on the stage of development of the first ring at the time of formation of the second tip flush, and that the intermediate boundary can be sharp only if the cambium has already formed late wood in the first ring. The same idea was expressed in the same year by Strasburger (1891) and later by Priestley (1928). Hence one finds all degrees of sharpness in this boundary from that of a typical annual growth layer to an invisible one. The botanical

literature is replete with descriptions, drawings and photographs of all intervening stages (Th. Hartig, 1837*a*, *b*; Nördlinger and Poirson, 1845; Unger, 1847; Wigand, 1854; Nördlinger, 1861; Ratzeburg, 1868; Goeppert, 1868; Ratzeburg, 1871; Nördlinger, 1872, 1874; Kny, 1879; Jost, 1893; Kühns, 1910; Späth, 1912; Sorauer-Dorrance, 1914; and many others). Quite similar conditions have been found to exist after defoliation by insects or storms (Kny, 1879; Wilhelm, 1883; R. Hartig, 1892*a*; Petersen, 1896; Lutz, 1897; Schrenk, 1898; and many others).

The number of additional growth layers present in a multiple series is usually one, that is, the layer is usually double. Three layers in one growing season are reported by Nördlinger and Poirson (1845), Unger (1847), Rossmann (1865), Ratzeburg (1868, 1869), Fernow (1887), Antevs (1917), Gates (1924), and by Illick and Aughanbaugh (1930); these cases are nearly all in native uninjured trees in the North Temperate Zone. Three rings a year are normal for some citrus fruits in California (Reed and MacDougal, 1937; Bartholomew and Reed, 1943). A number of instances of more than three growth layers in a single season have been reported in milder climates (Richard-Martins, 1864; Ratzeburg, 1866; Warring, 1877; Wright, 1901; Chamberlain, 1921; Child, 1882, 1883; Glock and Reed, 1940; Glock, 1951).

Do multiple growth layers usually accompany multiple tip flushes? If one may judge from the statements found in the more than 50 papers seen on this subject, there is no single answer to the question: often they definitely do, more frequently they do not. The problem was recognized at a very early period, Duhamel (1758) implying that second diameter flushes are present below all second tip flushes. John Hill (1770), who put the cart before the horse, stated that each time a growth layer is formed in the wood, the branch shoots out in length. All of the early workers reported such correlation, as Bechstein (1821), Hartig and Hartig (1836), Th. Hartig (1837*a*, *b*), in oak only; this generality is probably due in part to the fact that they did not consider a structure to be a second growth ring unless it was quite prominent. Later workers became more exacting. Their disagreement may also be attributed to failure to take into account the degree of maturity of the first tip flush at the time of beginning of growth of the second tip flush. And it may further be due to differences in

the part of the tree examined; it has been shown by Kny (1879), Jost (1891), Schrenk (1898), Kühns (1910), Späth (1912) and Wight (1930) that second growth layers often extend downwards on the branch only a short distance, usually not reaching the trunk at all and becoming progressively thinner downwards.

An opposite question is in order: are second growth layers formed without the presence of second tip flushes? Apparently they are not; they seem to be found only on branches below second tip flushes.

Little or nothing seems to be known about the formation of second diameter flushes in the cases of second flowering and fruiting (Gill, 1933), nor in proliferations in cones and compound fruits.

The causes which have been held responsible for the formation of multiple growth layers parallel very closely those which have been discussed for the production of multiple tip flushes. Our knowledge of the relation of growth hormones to cambial activity is as yet too meager to have been extended far into the problem of second growth layers.

Good discussions of multiplicity in diameter growth are found in Späth (1912, 1913), Antevs (1917), Küster (1925) and Büsgen-Münch-Thomson (1929).

GROWTH IN THE TROPICS

What would the botany of today be if all early centers of botanical research and most of the later ones had been located in the tropics instead of in the Temperate Zone? The many "irregularities" of growth in the tropics would, of course, have been considered "normal". Early botanists would have made only occasional excursions into the Temperate Zone to study the "abnormal" conditions found there, conditions which they may well have considered to be primitive because so much less complicated and more regular and uniform.

Such might very well have happened, for, as has already been shown, Theophrastus had at hand more information on semi-tropical and tropical plants than on those from farther north. And his work might well have been continued in Alexandria, Egypt, and spread from there to the south, east and west.

As it is, relatively little work has been done on plant growth in

the tropics. And there is much confusion because of the inability to give a clear definition to the concept, tropics. The areas generally included in the term range from perennially wet to alternating wet and dry to quite dry; from sweltering forest to scrub to grassland to desert; from sea level to perpetual ice on the high mountains. Most of the work done in these regions on tree growth has been purely descriptive of tip and diameter flushes, little or no correlation being usually attempted with total rainfall, seasons of rainfall, temperature or habitat. Therefore such excellent books as those of Gamble (1881, 1902) on the trees of India and of Record and Hess (1943) for the tropics of the New World lose much of their potential value unless the reader takes time to study the range, climatic conditions and habitat for each species—where this can be done. Nevertheless, descriptive work is quite valuable and has been accomplished with greater or less completeness in nearly all regions of the world which can be called tropical and subtropical: on the continent of Asia, in Java, Sumatra, India, Ceylon, Japan, Formosa, the Philippines and Aden; in Africa, the Libyan Desert, the Sudan, the Gold Coast, the Cameroons, Southwest Africa and the Seychelles Islands; in America, Brazil, Uruguay, Chili, Trinidad and tropical America in general; and in Australia, New Zealand and Hawaii. It is not intended to imply that there do not exist some excellent papers in which growth has been well correlated with climate and habitat; representative examples of such are those of Reiche (1897) in Chili, Simon (1914) in Java, Klebs (1926, etc.) in Java, Chowdhury (1939*a*, *b*, 1940) in India and especially of Coster (1927, 1928) in Java.

Certain changes take place gradually as one goes from the north toward the tropics. Theophrastus reported an increase in the number of growing periods from one or two in Greece to three in Crete and northern Egypt to four farther up the Nile; the length of the growing season also increases southward until it scarcely stops at all or is even continuous throughout the year; that is, the trees become evergreen. It is true that Theophrastus did not necessarily have the same species in mind, but he was able very definitely to see the tendency. Much later, and in the same region, Ascherson (1874) reported on a trip in the Libyan Desert; leaves remain on longer and longer as one goes south; one would imagine that they would reach an evergreen status near the equa-

tor. Büsgen-Münch-Thomson (1929) stated that species which are deciduous in Europe may be evergreen in the tropics. Timber transplanted from the north into the Malay Peninsula, according to Ridley (1901–1902), retain a tendency to form clearly-defined rings. In quite another part of the world, Penhallow (1907) reported on gymnosperms in a line from New York to Florida. He gives the constancy of the annual character of growth layers in the northern latitude as more than 99 per cent; the common red maple, *Acer rubrum,* which in the north quite generally forms a single ring in one year, will form at least 40 rings in less than 30 years in Florida.

The oldest known problem of tree growth in the tropics and the one which has received the greatest amount of attention is that of foliar periodicity. The contribution of Theophrastus to this phase of the problem has already been discussed. Then, after a lapse of many hundreds of years, botanical investigation in the tropics was revived by the explorations of Columbus, the Spanish, Portuguese, English and the French. There is reason to believe that a good deal of useful and interesting botanical information lies hidden in archives in Spain and Portugal, which have scarcely been touched by the botanist.

The topic of foliar periodicity has so often been summarized (Simon, 1914; Coster, 1927, 1928; Schimper-Faber, 1935; Weevers, 1949; Curtis and Clark, 1950) that a review here would be superfluous. The major topics involved are types of buds, number of tip flushes, gregarious flowering, limb-by-limb periodicity, continuous development, correlations with climate and the weather, and both external and genetic causes.

Study of growth rings in the tropics has been even more difficult than that of tip growth. This has come about mainly because of the complexity of leaf and twig periodicity, but also in part because of the almost complete absence of coniferous species, except in the mountains. Growth layers in conifers are generally sharply bounded, even in tropical mountains. On the other hand, broad-leaved trees show less sharply defined boundaries at best, and are especially indefinite in tropical regions, where they constitute almost the exclusive population.

It is not known who made the first comparison between growth rings in the Temperate and Tropical Zones. Link (1798) is said

by Bary (1884) to have reported total absence of ring boundaries in the "tropics". However, Ursprung (1900) noted that in a later edition, Link (1824) recognized rings as being present in warm regions but with boundaries less sharp than those in temperate regions.

Rest periods in cambial activity, with consequent formation of more or less well-defined growth layers, would be expected in tropical regions of alternating wet and dry climate. Brandis (1879) demonstrated the annual character of rings in a teak plantation of known age. In the same year, however, Fernandez (1879) claimed two rings a year for a teak coppice. Sharply bounded rings have been found in abundance in eastern Java, where a dry season is followed by one of alternating wet and dry periods, by Coster (1927, 1928) who has gone most deeply into the relation between growth layers and tropical climates. Similar situations have been reported from several parts of the world, especially where the second climatic period is more or less uniformly dry. Nevertheless, rings are also rather well defined in many species in the tropical rain-forest climate of central Java (Coster, 1927, 1928), especially in those species which range also into the eastern part of the island.

Growth layers in many tropical trees have, however, been found to be multiple. In the early part of the nineteenth century an argument raged long and very warmly as to whether the gymnospermous genus *Araucaria* has growth ring boundaries at all; and gradually other tropical trees were brought into the picture. An anonymous paper (1844) reports more than 60 rings in a 34- or 35-year-old baobab tree in Senegal, and Richard-Martins (1864) described one-year-old branches of *Phytolacca dioica* three to four meters long, grown in the Montpelier Botanic Garden, which had developed up to seven rings. One may wonder about the accuracy of a report by Warring (1877) on four in *Chenopodium*, especially as the place of growth and the habitat are not mentioned. It is quite certain that Charnay (1881–1882) was inaccurate in his interpretation of the 18 rings which he found on trees that had grown in excavated ruins in Central America (or Mexico) in a known period of 18 months; these must certainly have been the common concentric intra-annual lines so common in tropical wood (see below).

More accurate are some later reports. Baldwin (1884) stated that growth rings do not give the age of a tree in Florida. In dry central Uruguay, D. Christison (1891) reported an acacia tree six and one-half years old with 20 rings, another five years old with 40, and a specimen of *Melia* 11 years old with 18 rings plus nearly 100 very distinct " quasi circles ". In Brazil, J. Huber (1898) recorded that a planted one-year-old Hevea tree formed five end-on-end tip flushes from its terminal buds at periods 40 to 50 days apart; each time there was a lengthening of the axis, unfolding of the leaves, and a maturing of the leaves; after the leaves of the first five periods had fallen off, there were three more such tip growths, making a total of eight end-on-end tip flushes in one year. The same tree made three additional such end-on-end tip flushes during the next year. Multiple tip flushes in seedlings have also been recorded by Burgsdorf (1787) and by Th. Hartig (1859).

Following 1900 the number of papers reporting on the tropics is larger, many of them being on cultivated crop trees of known age and hence no doubt quite accurate.

Because of multiplicity, Coster (1927, 1928) estimated that ring counts in the tropics, when used in age determinations, represent an error ranging from very little for some species to 20 or 30 per cent for others. Under such conditions increment borings are of course of no value for age counts (Hutchinson, 1927).

The extreme opposite relation of growth layers to climate is reported by Holtermann (1902) for extremely dry Aden, where several years may pass without any rain; trees said by the natives to be 30 years old show only five or six rings, one ring apparently for each rain.

Even when growth layers are present in abundance and where their boundaries are relatively sharp, there is often little evidence that they are annual. They seem to vary with the vagaries of the weather, and the necessary careful work required in keeping records on individual marked twigs does not seem to have been done.

Factors and causes which have been assigned to cambial activity in the tropics do not differ materially from those assigned to growth layer formation in the Temperate Zone. The joint operation of several factors must, however, be far more complex. Coster

(1927, 1928) reported that growth rings are often correlated with tip flushes, as would indeed be expected from our present knowledge of the relation of growth hormones to cambial activity in the Temperate Zone.

In the tropical rain forest, certain species which are endemic there show continuous diameter growth. This means that the cambium continues its activity without a rest period at any time and that the wood may be a number of years old without showing any signs of ring boundaries. Continuous growth has been abundantly observed.

The anatomy of the growth layers of many tropical trees is far more complex than that of trees of the cooler zones. Such complexity can be only partially associated with climatic and weather conditions; it is largely inherent. A few examples, selected to show only the variations in the types of boundaries, are indicative of the anatomical complexities found in the growth layers. In "Timbers of the New World" by Record and Hess (1943), more tropical families are included than families of the Temperate Zone. The boundaries of the growth layers, when present, can be recognized in various ways, which we have summarized from a study of each individual description of the many genera in some 123 families, as follows:

I. Tracheids in conifers.—No information given, hence it is assumed that determinations can be made in the manner usual for this group.

II. Vessels.
   1. Ring-porous condition present to a greater or lesser degree; greater or lesser zonation in the early wood.
   2. Difference in density of the pores (much as in the preceding).
   3. Difference in size of the pores.

III. Wood fibers in dicotyledonous woods.
   1. Difference in radial dimension is sometimes limited to a narrow zone of late wood.
   2. Difference in wall thickness.
   3. Local difference in "density" (overlaps the two preceding).
   4. Prominent alternating bands of early and late wood.

IV. Parenchyma in the xylem.
   1. Presence of terminal parenchyma or of a narrow band of parenchyma.
   2. Wider spacing and more orderly arrangement of the parenchyma. Periodic wider spacing of parenchyma bands. Difference in the spacing of parenchyma layers.
   3. Presence of narrow bands of tissue deficient in parenchyma.

V. Late wood darker in color than early wood.

This summary of criteria for boundaries agrees rather well with a similar one which we have compiled from a study of 81 species in 61 genera in 29 families of Sumatra woods (Cockrell 1934):

I. Vessels: number, size, absence of, the more porous zone at the boundary, vessels in a zone of fibers, tangential band of vessels.

II. Fibers: change in density, radial flattening, thickness of wall.

III. Parenchyma: presence of terminal parenchyma, radial flattening of parenchyma cells, fewer parenchyma cells in outer part of the ring, greater abundance of metatracheal parenchyma at the boundary.

IV. Rays: flaring, distortion, or bending at the boundary.

Such a host of variations at the boundary alone can make the anatomy of tropical growth layers very complex, indeed. In many instances above, two or even several of these criteria may occur together at the boundaries of a single species. No effort was made by these authors to determine whether the growth layers are annual.

The reasons assigned for multiplicity of growth in the tropics run the usual gamut of drought, defoliation, food, heredity, etc. It would seem that the tropics represent a virtually unexplored field for work with growth hormones.

A significant aspect of the problem of tree growth in the tropics involves the reaction of native Temperate Zone trees when transplanted into a tropical region. Holtermann (1902) reported that such transplants to the tropics retain their periodicity for some time. Pfeffer (1903) stated that trees transplanted to different climates tend gradually to adjust themselves. According to Ding-

ler (1911), English oaks transplanted to the highlands of Ceylon show an irregular leaf and tip growth periodicity. Coster (1927, 1928) believes that conifers introduced from the Temperate Zone into Java retain their leaf periodicity; such transplants had, however, been made into the mountains. Many dicotyledonous trees, on the other hand, soon alter their leaf periodicity to one in which different limbs on the same tree lose their leaves at different times. On the whole, he finds in such transplanted trees a rather close relation between leaf periodicity and cambial activity, the latter not extending very far down the limb or very far into the trunk. While most introduced trees continue to form rings, they are often not annual and the sharpness of their boundaries is quite variable; there are also many intra-annual irregularities.

Reiche (1897) reported on transplants from the Northern to the Southern Hemisphere. He found that in general fruit trees transplanted from central Europe to subtropical Chili gradually become adapted to the seasonal changes in Chili, the peach becoming almost evergreen. The more recent literature on transplants into Australia, New Zealand and South Africa is along the same lines as the above.

A transplant from the tropics into the cooler zone was studied by Fischer (1905). A japanese larch, which in its native land presumably shows abundant multiplicity, retained this tendency in Germany, forming from one to six tip as well as one to six diameter flushes a year between the years 1898 and 1905.

Before arriving at conclusions on growth in the tropics, several recent papers merit brief mention in order to show the trend of research. Chowdhury (1939*a*, *b*) refers to continuous cambial activity in some species in India, and discontinuous growth in others. Walter (1940) finds a rather close correlation between precipitation and ring thickness in southwest Africa; the curve indicates a short weather cycle of 9.53 years and a longer one of 20.25 years. He extends the curve into the future and makes a tentative weather forecast from it. I. W. Bailey (1944) finds that ring boundaries vary from good to absent in the tropical family Winteraceae. He concludes that there are two distinct types of zonation phenomena in wood: (*a*) obligate rings, as those in many trees of the Northern Hemisphere; and (*b*) facultative rings, like those in many plants of tropical and subtropical regions as well as plants of the Southern Hemisphere, in which the formation of

boundaries is entirely dependent upon the environment. On the Gold Coast of Africa, Hummel (1946) finds growth layer boundaries not only often present but in many cases of an annual character, so that ring counts may be expected to give a fairly reliable estimate of age in some species. In other species the cambium is active twice a year, and in certain others cambial activity is variable from year to year. Often many intraseasonal irregularities, such as bands of varying sharpness, are present, and cambial activity often follows the flushing of leaves. Jane (1934) and Chowdhury (1947, 1953) find initial parenchyma to constitute a very common type of boundary in the tropical trees of India; it had previously been supposed that this tangential layer of parenchyma is always formed at the close of the growing season, in which case it is of course terminal parenchyma. Chowdhury (1939*a*) had already called attention to the incorrectness of our usual interpretation in the genus *Terminalia*. Humphries (1947), working with the cacao tree in Trinidad, shows that starch is used up as the cambium becomes active; there is no real rest period of the cambium, although there are several cycles of growth each year.

Certain conclusions may be derived from the work on the growth of trees in the tropics. Multiplicity is rampant in both tip and diameter growth. At least in most species, none of the usual methods of determining age can be relied upon. There is usually little reliable correlation between growth and climate, growth and weather, or between tip growth and diameter growth. It is probable that the tropics will prove to contain the most promising geographic regions for solving some of the complicated problems of both tip and diameter growth in trees and shrubs.

GROWTH OF ROOTS

The underground parts of plants have never received the attention which they deserve. Their unpopularity is of course due to the difficulty of studying them in their native environment. This applies not only to the roots of trees, but to other roots as well, and to rhizomes, bulbs and corms.

Because their environment, the soil, is much more uniform than the aerial environment of the stem, the growth responses of roots are in many respects comparable with those of stems in a tropical rain forest. This is true of both length and diameter growth.

It is difficult to find a botanical subject which was not touched upon by Theophrastus. In his "Enquiry into Plants" (Hort, 1916) we find the statement that no root goes down farther than the sun reaches, since it is heat which induces growth. And in the "Causes of Plants" (Dengler, 1927) Theophrastus tells us that he did not completely agree with those who said that roots grow in the fall and winter, while trunks and branches grow in spring and summer.

Indeed, the question of periodicity in length growth has been one of the major research problems on the roots of forest trees. The problem interested the French botanist and forester Duhamel (1758, 1760) who found growth to occur during the winter. There is, however, no definite period of length growth for all trees, although much of it does actually take place in the autumn and even through the winter, often in several growth spurts. The result is, of course, multiplicity in length growth, although the boundaries between the successive tip flushes are poorly defined or not at all. Roots are much more likely to die back than are stems, which adds to the complexity of studying their tip flushes. When root growth is described, especially as occurring in the winter, it may mean length growth of the tap root or of already existing lateral roots, or the formation of new lateral roots, or both tip and diameter growth. The bud-root theory of root growth has been discussed earlier in this paper.

Relatively little is known about diameter growth in roots. Multiplicity is quite common, as are also many types of partial rings and indistinct boundaries.

A closer study of roots should also help solve some of the fundamental problems of tree growth. Many of these problems are summarized by Bischoff (1836), Mohl (1862), Engler (1903), Hilf (1927), Lodewick (1928), Büsgen-Münch-Thomson (1929), MacDougal (1938), J. F. Reed (1939) and Kramer (1949).

It is of interest that Grew (1682) first used the word "cambium" in a study of the anatomy of the root.

CAUSES OF GROWTH

The causes of growth can not be discussed without a definition of terms. To the layman, resumption of growth in spring is caused by the rise in temperature; to the botanist, the problem of tem-

perature has receded from a cause to a mere modifying factor. This has been the fate of nearly all "causes". At the present time, growth hormones are considered causal, but it is very probable that they, too, will become merely important factors when we possess more fundamental knowledge about them.

It is not our intent to review either the "factors" or the "causes" of growth, for these may be found in many modern textbooks of plant physiology and plant ecology, as well as in the histories of botany. An excellent summary is contained in Büsgen-Münch-Thomson (1929). We desire, instead, to call to the attention of the reader several forgotten chapters in the history of our knowledge of plant growth.

We return once more to Theophrastus' "Enquiry into Plants". In the translation into German by Sprengel (1822) we find this statement: "If one permits the buds to remain on the trees, the latter grow rapidly in length; if they are removed early, the trees become more compact, like the grapevine". According to Ernst Meyer (1832), Duhamel reported at the middle of the eighteenth century that length growth of the horse chestnut is stopped by cutting off the tip at an early stage while still in the herbaceous condition. And Burgsdorf (1783) said that leaves are most important in that they precede all development in the mature plant; each leaf furnishes the materials needed for the growth of the node below it.

Credit for having first suggested that growth may be due to a stimulating substance (hormone), not merely to food materials, is given to Sachs for the year 1880 by Möbius (1937) and to Charles Darwin for the year 1881 by Crocker (1948). Mer (1892) believed that the differences between spring and summer wood are to be explained by the plastic materials (as opposed to foods) which become available to the cambium. Coster (1928) expressed the opinion that some substance or stimulus originating in the developing leaves and passing downwards through the phloem is responsible for initiating the growth of the cambium; this stimulus, which is not a reserve or a new food, he believed more likely to be a hormone. However, as is often the case, the practical farmer anticipated the scientist. There was in use in France a horticultural practice which involved external application of some type of "growth substance". In the Oelhafen translation of

Duhamel into German (1765), we find the following: "Some writers recommend that the end of cuttings be dipped in a certain mastic salve, whose preparation is described with much circumstance; they claim that it results in the rooting of the cuttings. I have tried this suggestion, but believe that the formation of the swelling which precedes the new roots was somewhat delayed, since the swelling, instead of being formed at the end of the cutting, was formed above the putty [used instead of grafting wax]. Therefore, I concluded that the method at least did no good, and may be damaging". Information on the contents and the method of preparation of this concoction would be of considerable historic and scientific interest; since its use was apparently a somewhat common practice, at least in France, it should be found in the French horticultural literature of the day.

A stimulus, although not in the sense of a hormone, is referred to by Hundeshagen (1829); he considered the possibility that one cause of multiplicity in tip flushes may be the stimulating influence of the increase in sap flow at that time of year.

One very sugary morsel of history has apparently been completely missed by the reviewers of botanical literature. In 1868 the German plant physiologist Sachs (1868) postulated a theory that bark pressure is the cause of the difference between spring and summer wood. His statement is as follows: "The cause of this difference has not been heretofore known, but I would guess that it is simply dependent on changes in the pressure exerted on the cambium and wood by the surrounding bark; this pressure is less in the spring but becomes increasingly greater toward the autumn; I do not have direct measurements, but arrive at this conclusion from the fact that the longitudinal splits in the bark made in February and March become broader, as seen clearly in *Quercus, Acer, Populus, Juglans,* etc.; I will not discuss the causes of this increase in pressure, but nevertheless, the bark, whose longitudinal splits have become widened during the winter, exerts a diminished pressure on the cambium in the spring, so that the wood cells are then more easily enabled to expand radially; the pressure on the cambium must then constantly increase because of the thickening of the woody cylinder on one side and the drying out of the bark during the summer on the other side, and accordingly decreases the radial growth of the young autumn wood cells.

Further investigations, which I am planning, will show whether my theory is correct". (In Sachs' day it was thought that the late wood is formed in autumn). Later, Vries (1872*a*, *b*, 1875, 1876) presented what seemed to be incontrovertible proof of Sachs' theory, which the latter author repeated in later editions of his physiology text. Some years later, however, measurements made by Krabbe (1882, 1884) showed that, although bark pressure does indeed exist all through the year, the difference in the measured amount of pressure during the different seasons is far too small to account for the differences between spring and summer wood.

This much is a well-known part of the history of botany. But Sachs, "author" of the bark pressure theory and the historian of botany, had the misfortune altogether to miss the fact that his theory had been brought forward in considerable detail just 85 years before he made his own suggestion!

We have already met Burgsdorf in several connections in this paper and shall meet him again. Although his name does not appear anywhere in Sachs' "History of Botany, 1530–1860" (translated by Garnsey and Balfour, 1906), to Burgsdorf seems to go the credit for having first proposed bark pressure as the cause of tree rings. In reading his statement of his theory, it should be remembered that the cambium was not considered to be a tissue in his day and the splint, a term applied to the inner layer of "bark" was believed to become converted into true wood. Translated, his statement is as follows (Burgsdorf, 1783, pp. 232–233):

> The growth of this young splint continued until the sap becomes concentrated in the late autumn, the twig having long before completed its growth in length.
>
> Now, the more the splint hardens on the outer face of the true wood, and the smaller the amount of sap which passes through it, the more does this coat [splint], together with the bark, pull itself together, since the causes for further expansion have now been removed; rather do these causes now result in a coagulation of the small amount of sap present.
>
> So there comes about a drawing together and a pressure from the outside, from the circumference toward the center. The splint of the preceding year becomes compressed evenly, and it, in its turn, presses evenly on the pith.
>
> All of the tissues inside of the new splint therefore become more dense, being surrounded by the young hardening splint; and the outermost part of these inner tissues now becomes true wood which differs from the splint only in its greater density and dryness. Because the pressure of the splint

on the wood operates most effectively on the outer surface of the wood, there is produced at that surface the much denser layer [late wood] which represents the identifying characteristic of the ring. . . .

In his second volume, Burgsdorf (1787, pp. 94–95) used his pressure theory to explain the conversion of white wood (sapwood) into ripe wood (heartwood); and again (p. 100) we find the statement that as the inner bark dries it is constantly compressed inwardly.

Although Burgsdorf did no experimental work, his statement of the pressure theory as applied to the formation of growth layers is as clear as is that of Sachs—who also had done no experimental work on the problem.—The light of Burgsdorf should shine much more brightly on the pages of botanical history. Sachs can be forgiven in part, for all of Burgsdorf's statements used in the present paper are well hidden, with no suggestion of their presence in the titles of his books, nor in his chapter headings; and since there are no indexes, they can be discovered only by stumbling upon them.

Willdenow (1792) expressed much the same idea as did Burgsdorf, only much less clearly: "A new circle of vessels [all elongated cells in the wood] is formed annually in the stem around the older circle, which crowds the inner circle closer together . . . in the course of time, however, several circles of vessels have become formed, which crowd the innermost circle into greater compactness . . .". At another location he considered bark pressure to be the cause of thin rings: "If the bark is too firm, then there are formed annually only thin wood rings", both in trees and in shrubs. A few years later Cotta (1806) held that the change from splint to wood, the wood being denser and harder, could in no wise be the result of a greater pressure from the outer parts, for in that case transition could be only gradual and thus could not result in the sharp boundary between splint and wood (i.e., between two adjacent rings). Theodor Hartig (1860) maintained that there is no bark pressure at all in trees during the summer. Almost simultaneously with Sachs, Kraus (1867) showed that an enlarging stem does exhibit bark tension in the summer, but he did not obtain quantitative results of value. Nördlinger (1870) showed the presence of bark pressure during the summer in pine, larch, birch and oak. The same author (1872) also showed that rings become thicker after ripping of the bark and releasing of the

pressure on the wood. Again two years later, he (1874) disagreed with Vries (1872). N. J. C. Müller (1876) considered bark pressure to be the cause of ring formation. A few years later, Nördlinger (1880) modified his view somewhat; although he considered bark pressure not to be the cause of growth rings under normal conditions, there are many cases, he said, of wavy outlines in trees, shrubs and vines, as seen in cross section, which are best explained by supposing them to be due to irregularities in bark pressure. Penhallow (1885) did not believe bark pressure always to be applicable. Janowitsch (1895) also dealt with bark pressure. Schwarz (1899) discussed the power of the plant to react to bark pressure, and Sorauer-Dorrance (1914) followed Vries and discounted Krabbe.

Thus we find that, preceding Sachs' first statement of his idea, the same thought had been mulled over by Burgsdorf, Willdenow, Cotta, Hartig and Kraus.

INTERNAL MARKERS

The problem of dating an individual growth layer in a tree with absolute certainty is a difficult one. A simple counting of rings is, of course, quite uncertain, since there is always a possibility that multiple rings may be present, or even that the cambium may have failed to lay down a growth layer at all during a given year. In anatomical work it is often necessary to know the date of a specific ring, or it may be desirable to know whether during a given year one or more or perhaps no ring had been laid down by the cambium.

Among the several methods by which such determinations may be made with absolute certainty is that which may be called "internal markers". In its simpler form the method is very old and consists of finding some mark which Nature herself has placed in the wood of a tree at a known time. The literature on this subject is extremely voluminous, including, as it does, identifiable rings resulting from defoliation, drought, fire, lightning and unfavorable weather conditions. Dating back to the severe winter of 1708–09 will be discussed in the next section. Although Theophrastus did not know that the date of growing together could be determined by counting the superimposed growth rings, he nevertheless made this interesting comment (Sprengel, 1822): "For it

often happens that one part of a tree, which has grown together with another part, becomes enclosed by the latter". Waterhouse (1811) said: "Who knows, but we may hence form a probable conjecture of the age of those surprising antiquities [Indian mounds], discovered in this new world on the banks of the Ohio and Muskingum?" Agardh (1829, 1830), living in an age when the world was still believed to be only 6000 years old, spoke of the possibility of using trees to tell us the age of coal measures, limestone strata, etc. Similarly, Candolle (1827, 1831, 1833*b*) suggested the use of tree rings for determining the age of monuments, of talus slides, of changes in dunes and river beds, of the origin of volcanic and coral islands, and of the "last revolutions of the globe" (cataclysms).

Hough (1882) believed from a study of sections of tree trunks in museums that it is possible to date accurately insect injuries of a century or more back by certain characteristic thin rings. Baldwin (1884) reported that Prof. Jeffries Wyman proposed to reach a conclusion of the approximate age of some Indian mounds in Florida by counting the rings of trees growing upon them; this was probably not done, for Baldwin had called his attention to the inaccuracies inherent in the many multiple rings present in the trees of Florida. Robert Hartig (1892*b*) used hail injury of a known date to determine whether annual diameter increments had reached the base of the trunk in closed pine stands; he found five growth layers to be absent at the base. Similarly, Rubner (1910) used natural frost injury to date the rings formed above and below a constriction placed on the trunk. I. W. Bailey (in Swaine, Craighead, and Bailey, 1924; Bailey, 1925*a*) employs natural frost rings in determining the dates of certain growth layers. In the first paper just mentioned (1924), as well as in a later one (Bailey, 1925*b*), he relied on abnormal growth rings caused by insect defoliation as a criterion of age. Glock and Studhalter (1948) discuss natural frost rings as a tool in dating, and Glock (1951) elaborates further on the idea. In fact, the entire method of cross-dating by use of narrow rings is a part of this phase of the problem.

In an excellent piece of work, Enos Mills (1904, 1908, 1909*a*, *b*, 1914) dissected a large yellow pine, *Pinus ponderosa*, in the Rocky Mountains and reconstructed its life history from internal

evidence. His conclusions were based on the belief that each of the 1047 growth rings represented the diameter increment of a single year. At 135 years of age, some limbs broken off of a falling neighbor were embedded in the old pine, to be covered over in 12 years. A year or two later, ants and borers became active, their activity soon to be reduced by birds (woodpeckers, etc.). It was struck by lightning at the end of the summer of 1301. Checking and shattering between 1811 and 1812 are interpreted as having been caused by an earthquake shock. Also between 1811 and 1812, a five-pound stone bounding down the mountain side struck the tree so violently that it became embedded; it ultimately became healed over and remained hidden until Mills found it. This is only a single example, a rather early one, of trees for which life histories have been read from internal evidence.

Of greater significance, perhaps, and certainly of greater human interest, are internal markers of one kind or another which man himself has deliberately placed into the trunk or branch of a tree. For the first such case on record we must go once more to Theophrastus (Sprengel, 1822; Hort, 1916). We find this statement: ". . . and if one forces a stone or some similar object into a tree, it becomes hidden, since the new growth surrounds it, as was the case with the wild olive tree which stood in the market place at Megara". While the purpose of forcing the stone into the tree is not stated, the conclusion that new wood is deposited over the old is inevitable.

The indefatigable Duhamel used internal markers in many of his experiments in an effort to determine how the new bark and new wood are formed. In one set of experiments (Duhamel, 1751) he described the placing of small strips of tin foil at definite depths in the cut bark or cut wood, tying the bark and wood back into place, treating with an antiseptic, and examining again at the end of the growing season. In other experiments, fine silver wires were forced through the bark and wood at approximately known depths. He was able to draw important and mostly correct conclusions about the manner of growth of both bark and wood. The experiments are again described in his classical "Physique des Arbres" (Duhamel, 1758) and in the Oelhafen translation into German (1764, 1765).

The carving of dates, initials and other markings through the

bark of a trunk is another example of this method. Burgsdorf (1787) used an axe mark of a known date, namely, August, 1767, on an oak tree at a boundary line as proof that only one ring is formed each year; in November, 1785, the blaze was covered by 18 growth rings. Goeppert (1868–1870) cited many cases, beginning with Bartolinus in 1654, in which inscriptions through the bark of trees as well as monuments (the nature of the latter not explained) were used in proving that growth layers are annual, for in every case the number of layers corresponds with the number of years which had elapsed from the date of the inscription or monument. The same method had already been used by Candolle (1827, 1828, 1831, 1839, 1839–1840), described by Bischoff (1836), Jussieu (1843), Nolte (1846), Lindley (1848), Jaschke (1859) and Ratzeburg (1866), and long ago suggested by Schober (1753).

Numerous legal cases involving property rights have been settled in court from the blazes left by surveyors on the trunks of trees along boundary lines (P. C. Smith, 1883; Child, 1883; Hotchkiss, 1894; Fernow, 1888, 1897). In nearly all cases the court accepted the dictum that tree rings are annual; however, at least one case is on record (Child, 1883) in which the court ruled that growth layers are not infallible indicators of age. A case was recently brought to court in Alsace in which tree rings were used as evidence of ownership (Senn, 1933). Tree rings were used also by Tharp (Sellards, Tharp, and Hill, 1923) in a boundary dispute between the States of Texas and Oklahoma, and by Cowles (1915) in an extensive Federal lawsuit in Arkansas involving riparian boundaries.

In interpreting the life history of the old yellow pine mentioned above, Mills (1909, 1914) interpreted several situations as internal markers placed by man. In 1486 two flint arrow heads became embedded in the wood, suggesting a bear hunt or an Indian battle. A basal fire scar in 1840 may have had its origin from a camp fire of the early Spaniards. An axe mark of 1859 was probably a trail blaze. A similar fire scar in 1859 probably originated from a prospector's camp fire. In 1881 several rifle bullets became embedded around and just beneath a blaze; Mills suggests target practice as a possible explanation.

In experiments on double rings after artificial defoliation, Wil-

helm (1883) marked three places on each of seven- to nine-year-old oaks by cutting out a piece of the bark to the cambium and smearing tar on the wound; the same was done with control trees. Later examination revealed the extent and kind of growth after the date thus definitely established.

Glock and Studhalter (1941), who used the term "internal tagging", briefly discuss frost injury artificially induced in the branches of Arizona cypress, and Studhalter and Glock (1941, 1942) describe a newly designed simple apparatus for the purpose, using dry ice as a refrigerant. The same authors (1948) further discuss artificial frost as a tool in dating the growth layers in trees (also Glock, 1951).

Brumfield (1943) has utilized a form of internal tagging in the study of cell lineages in root meristems; certain chromosome rearrangements induced by x-rays were used to tag a single cell and to determine the kind and extent of tissues which were derived from it.

Carbon dating with C^{14} can be of value only in older trees. It has been successfully used on old timbers (Libby, 1952).

The discovery and use of additional tagging methods should be a fruitful field for research.

CROSS-DATING

The term "cross-dating" means the comparison of identifiable characteristics of rings in two or more trees, with the result that it is possible thereby to assign dates to the various rings. The method, as used today, generally involves characteristic thin rings which result from the meager diameter growth during periods of rainfall or soil moisture deficiency.

From an historical point of view, the principles of cross-dating could not become scientifically established until the manner of growth of tree rings was well understood by the botanist. The early history of our knowledge of the annual character of growth layers was followed by the simple procedure of dating past events by counting the tree rings backwards from a known date.

This was apparently first done by the Frenchmen Duhamel and Buffon (1737) who counted back to the wood ring of 1709, in which was found a severe frost injury, called "false sapwood" by

them. The winter of 1709 was known to have been very severe, and the false sapwood was supposed to have been caused by the severity of the winter. It appears to have been a common belief at that time that wood continues to grow through the winter, or at least far into this season; it would be natural, therefore, for botanists to attribute any abnormality in a ring to the severe cold of the corresponding winter. Duhamel (1758) repeated a statement of this work many years later.

Just a few years thereafter we find Linnaeus (1745, 1751) in Sweden arriving at the identical conclusion, and also counting the rings back to the severe winter of 1708–1709, for which he found a very thin ring. Only a single stump was studied. He went a step further than Duhamel and Buffon in that he spoke of tree rings as the chronicles of winters (Linnaeus, 1777, according to Wastenson, 1927, and Erlandson, 1936), and apparently he retained this opinion to the end of his life.

Burgsdorf (1783) also counted back to the winter of 1709, whose ring he described as having a freezing injury. Likewise, Candolle (1839–1840) stated that he had in 1800 counted back 91 woody rings on a specimen of *Juniperus communis* in the Forest of Fontainbleau to the frost injury of the severe winter of 1709; a rather poor illustration accompanies the statement.

The several observations just mentioned indicate that the winter of 1708–1709 was a severe one, at least in France, Sweden and Germany, and written historical records bear this out. In a sense, these data could, taken together, be considered as the beginning of cross-dating, for they all go back to the same year, even though the backward count started on different dates.

The further observations of Burgsdorf (1783) prove very definitely to be cross-dating, which was done consciously and based on his own work. He stated that (*a*) frost damages the bark and may also injure the wood; (*b*) sometimes one finds dead and decayed areas enclosed within the normal healthy wood, which has grown over them; and (*c*) according to ring counts, this condition occurred in the winter of 1709 *in beech and in most other trees* (italics ours). Thus he compared several trees and several species, and fulfilled all of the criteria laid down in the first paragraph of this section for cross-dating. Indeed, to Burgsdorf should go

the title of Father of Cross-dating. It is our judgment that this man, who was so completely ignored by the historian Sachs, deserves a large place in the history of botany.

In 1827 Twining (1833) rediscovered the very essence of cross-dating. It is worth while to quote his entire brief article because it is so full of pregnant ideas:

I take this opportunity to mention a fact, which I once observed, and which may, perhaps, prove interesting to the readers of your Journal and lovers of natural science. In the year 1827, a large lot of hemlock timber was cut from the north eastern slope of East Rock, near New Haven, for the purpose of forming a foundation for the wharf which bounds the basin of the Farmington Canal on the East. While inspecting and measuring that timber, at the time of its delivery, I took particular notice of the successive layers, each of which constitutes a year's growth of the tree; and which, in that kind of wood, are very distinct. These layers were of various breadth, indicating a growth five or six times as full in some years as in others, preceding or following. Thus, every tree had preserved a record of the seasons, for the whole period of its growth, whether thirty years or two hundred,—and what is worthy of observation, *every tree told the same story.* Thus, if you began at the outer layer of two trees, one young and the other old, and counted back twenty years, if the young tree indicated, by a full layer, a growing season for that kind of timber, the other tree indicated the same.

My next observation was, that the growing seasons *clustered together*, and also the meagre seasons came in companies. Thus, it was rare to find a meagre season immediately preceding or following a season of full growth,—but, if you commenced in a cluster of thin and meagre layers, and proceeded on, it gradually enlarged and swelled to the maximum, after which a decrease began and went on, until it terminated in a minimum.

A third observation was, that there appeared nothing like *periodicity* in the return of the full years or the meagre, but the clusters alternated at irregular intervals; neither could there be observed, in comparing the clusters, any law by which the number of years was regulated.

I had then before me, therefore, two or three hundred *meteorological tables*, all of them as unerring as nature; and by selecting one tree from the oldest, and sawing out a thin section from its trunk, I might have preserved one of the number to be referred to afterwards. It might have been smoothed on one side by the plane, so as to exhibit its record, to the eye, with all the distinctness and neatness of a drawing. On the opposite side, might have been minuted in indelible writing, the locality of the tree, the kind of timber, the year and month when cut, the soil where it grew, the side and point which faced the north, and every other circumstance which can possibly be supposed ever to have the most remote relation to the value of the table in hand. The lover of science will not be backward to incur such trouble, for he knows how often, in the progress of human knowledge, an observation or an experiment has lost its value by the disregard of some circumstance con-

nected with it, which, at the time, was not thought worthy of notice. Lastly, there might be attached to the same section, a written meteorological table compiled from the observations of some scientific person, if such observations had been made in the vicinity. This being done, why, in the eye of science, might not this *natural, unerring, graphical* record of seasons past, deserve as careful preservation as a curious mineral or a new form of crystals?

If you should think fit to make such a suggestion, it might lead, in fact, to the preservation of sections from aged trees in different parts of the country, and a comparison of their lines of growth with the history of the weather as far back as our knowledge extends. If the observations just related, with respect to a particular lot of timber should be found to hold true of trees, in general, drawings of these sections, on a reduced scale, would soon find their way to the pages of scientific journals. It would be interesting, then, to make comparisons of one with another,—to compare the sections of one kind of tree with that of another kind from the same locality, —or to compare sections of the same kind of tree from different parts of the country. Such a comparison would elicit a mass of facts, both with respect to the progress of the seasons, and their relation to the growth of timber, and might prove, hereafter, the means of carrying back our knowledge of the seasons, through a period coeval with the age of the oldest forest trees, and in regions of the country where scientific observation has never yet penetrated, nor a civilized population dwelt.

Here, indeed, we have not only cross-dating with a vengeance, but a prophetic insight into the future.

The story of the cross-dating done by Kuechler (often misspelled Keuchler) on oaks at Fredericksburg, Texas, in 1859 has been told several times (Glock, 1941). Some recent papers bring our knowledge of the man and his work up-to-date. Lowry (1934) studied some oaks cut in 1934, also at Fredericksburg. For the years in which his rings overlap those of Kuechler, there is some similarity between the weather data inferred by the two men. But Kuechler (1859) obtained far too many wet years, a fact which has not hitherto been explained. A comparison between the climates of Texas and Germany may furnish a clue to an explanation. The Fredericksburg area in Texas lies so much further south than does any part of Germany, in which country Kuechler obtained his training in forestry, that the Texas growing season is no doubt much longer, and probably the rings correspondingly thicker. If this assumption is correct, Kuechler must have been accustomed in Germany to oak rings which average much less in thickness than do those in Texas, and when he saw the thicker Texas rings, he assumed them to be due to wetter

years. Hence he would interpret his data as indicating a disproportionately large number of very wet seasons.

Campbell (1949) succeeded in finding the original article of Kuechler's in the archives of the University of Texas; he calls attention to certain errors promulgated by later commentators. He also adds a good deal of information on Kuechler's life and public activities.

In the same year that Kuechler wrote his article in a newspaper in Texas, Vonhausen (1859) published a somewhat similar article in a professional journal in Europe. Based upon measurements of ring thicknesses in a half dozen species of trees, he found the ring of 1858 to be thin because the preceding late summer, winter and spring had been very dry. In every case where the same tree was used, there was less diameter growth in 1858 than there had been in 1857. He adds that the narrow ring will be recognized in the trunk many years later.

In commenting on Vonhausen's paper, Nördlinger (1874, footnote page 166) stated that "It would seem to be desirable, in consideration of these [external] influences, to study the correlation of all narrow rings with all dry winters of the past".

The suggestions of Twining and of Vonhausen seem to have been almost completely forgotten. Similar suggestions made independently by Pokorny (1865–66) have recently been resurrected. This writer states that since climate is one of the most important factors in determining diameter growth, it follows that the characteristics of the weather of each year must be distinctly reflected in the structure of the wood ring. If this is true, the rings would become true meteorological yearbooks which, because of the great age of many trees, would date back not only for centuries but for millenia. He proposes a comparative study of the annual rings of the same given year in different trees, and he himself did just enough experimental work to show the feasibility of the method. A year later Pokorny (1867) again spoke of tree rings as meteorological yearbooks, going back hundreds and even thousands of years.

L. H. Bailey (1885) echoed the statement of Twining when he wrote that by their thicknesses tree rings are "meteorological records of the years". Similarly Baldwin (1884) stated that a tree represents a true record of the weather, in so far as drought and rainfall are concerned.

In a later paper Pokorny (1869) gave more specific directions for the study of cross-dating although, of course, he did not use this term. And he recommended the study of as many rings as possible with the microscope. He concluded that if these ideas are applied, trees may indeed give us the hope of obtaining information on the weather of individual years several thousand years ago. He was well aware of the disturbing influence of such factors as exposure, defoliation and the course of nutrition. Nördlinger (1872, 1874) was much less charitable toward Pokorny than he was toward Vonhausen. In fact, the objections of this well-known botanist were so strenuous that one wonders whether he did not succeed in nipping the newly proposed science of cross-dating in the bud.

Elias Lewis (1873) made the interesting comment that it had long been customary to make estimates of the ages of many standing trees from the number of rings on another tree in which rings could be counted. Ratzeburg (1866) compared the ring of a certain year, the result of caterpillar injury, in different trees, thus dating these rings absolutely. R. Hartig (1897) also used the exact principle of cross-dating in determining the age of trees killed by smoke and fumes, only that he compared two different levels of the same trunk instead of comparing two different trees. Actual ring counts at the base often proved to be impossible because of the frequent omission of rings at that level. First he selected characteristically thick and thin rings in the upper part of the bole, where he assumed all rings to be present. The number of rings formed between these characteristic rings was accurately counted. Then, at DBH on the lower bole, he located the same characteristic thick and thin rings, and interpolated the number of intervening rings from above. This gave him a close approximation of the age of the tree at its base. Andrews and Gill (1939) called attention to the fact that this is almost exactly the method used by the dendrochronologists.

Schwarz (1899) made a large number of comparisons of ring thicknesses in different pine trees for the same year, but did not seem to look upon the problem as one of cross-dating.

The astronomer Kapteyn (1914) brought out a long unpublished paper on cross-dating work on oaks in Holland and Germany, done in the year 1880. One of his conclusions is that fluctuations in ring thicknesses are due largely to subsoil moisture,

especially from spring and summer rains. Kapteyn compared the ring thicknesses from tree to tree, and therefore succeeded in doing true work in cross-dating.

Lakari (1915) in Finland determined which years between 1757 and 1900 had been good seed years in pine. A good seed year covers a large geographical area, and following such a year a large number of trees should have the same age, since they started together; ring counts showed this to be true. A similar situation exists in an area of lodgepole pine coming in after a fire, and in certain desert trees which are able to become established only after several successive years of heavy rainfall, which in the desert is a rare occurrence. A comparison of ages in these cases by ring counts is, of course, cross-dating.

This account brings the history of cross-dating up to the work of A. E. Douglas in the American Southwest, work which began about 1904. It shows that the idea has occurred independently to several men in different countries and over a period of many years. It remained for Douglas, however, to use them extensively and to apply them widely to astronomy and to archaeology.

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II. Growth Rings and Climate

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"... to the naturalist the virgin forests of Borneo are still a wonderland full of strange questions and half-suspected discoveries."
—H. G. Wells.

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INTRODUCTION

Since the previous review was prepared (Glock, 1941), growth-ring studies have developed apparently along several trends: *a*) gathering of large collections of samples which cut across hundreds of miles of diverse topography, climate and soil in order to detect possible general fluctuations of climate; *b*) lessening reliance on long-time dating; *c*) lessening emphasis on growth layers as exact rain gauges; and *d*) increasing emphasis on the study of growth layers through botanical disciplines.

It is not the intention of the writer to review all articles pertaining directly to the subject because in 30 years his bibliography has grown to thousands of entries, and even the last 12 years have added more than can conveniently be incorporated here. His purpose, rather, is to trace major developments. An excellent though brief summary and discussion of current work in growth rings have been given by Dobbs (1951). In addition, criticism of specific points has been made by Glock (1942*a*, *b*) and by Sampson and Glock (1942).

Sincere gratitude is due the Smithsonian Institution and Macalester College for the financial support which made the review possible. Also, I am deeply indebted to many friends who, knowing of my interest in growth layers, were constantly on the watch for publications and information pertinent to my interests. For many hours of editorial assistance I am extremely grateful to Waldo S. Glock, Jr.

Zeuner (1950*b*) wrote: "The twentieth century is characterized by an expansion of prehistoric research . . .". To this expansion the study of growth layers, or tree rings, has contributed a share not only from the human and chronologic but also from the climatic standpoint. Both have exhibited extreme claims and conservative cautions; the truth very probably lies between the two.

The mathematical and dynamic approach to the study of tree growth could conceivably be the logical one (Haskell, 1940) because organisms are integrations of a pervading environment, physically and chemically, and because " the second law of thermodynamics implies universally increasing complexity" among plants and animals. At least one writer maintains that " his interest in dendrochronology lies largely in its possibilities as a branch of physical science " (Schulman, 1945*a*). Perhaps this non-biological

approach to biological problems was of concern to Davis in 1889 when, in discussing pine trees, he asked: "Why not [speak] of other vegetable growths, with straight vertical axes, from which lateral arms spread out with some regularity, bearing long, slender spicules on their minuter divisions?" (Davis, 1909).

Chronology of past events may not be of vital importance to the world today, but it is none the less a fascinating subject. Even the life history of a single pine as read by Mills in 1909 carried an interest not to be evaded. He completely dissected the tree—trunk, limbs and roots—and counted 1047 rings of growth at the base. It probably sprouted in 856 A.D. Then Mills chronicled an eventful life: at year 20 snow bent the tree; at year 135 it was stabbed by the dead limbs of another tree which fell against it; lightning struck it in 1301; two large limbs were lost in 1348; in 1486 two arrow heads were shot into the tree; in 1540 it felt steel and fire; in 1762, in 1804 and in 1805 climatic stress assailed the tree; in 1859 an ax left its mark; and in 1881 several rifle bullets penetrated the wood.

Dating the Indian Pueblos of the Southwest has constituted a romantic episode in the study of American prehistory. Such dating assumes positive identification of the annual increment of growth and relies upon a so-called master chart which represents an amalgamation of tree-ring sequences of varying length locked together over the centuries, some intervals built on many sequences, others on few. Even granting the accuracy of the chart and its wide areal applicability, and disregarding botanical and ecological questions, we encounter claims that seem unnecessarily extreme. For instance, dating has been called nearly miraculous (Davis, 1931); "one of the most important developments of modern science" (Gilpin, 1941); magic, a miracle (Abbott, 1946); a problem solved (King, 1951). Hawley (1939) stated that at first tree-ring analysis sought help from other sciences but that now it is itself a science and, "year by year, offers new application of its adaptable technique to problems in the very sciences which originally set it upon its now steady feet".

In contrast Gladwin (1943) had difficulty in reconciling certain tree-ring dates with the archaeological evidence. His appraisal of the dating situation had perhaps raised a needed caution signal. The time subject in the synthesis of a culture, he said, must "be

regarded as an intangible" one "in spite of the tree-ring dating". As regards the assignment and expression of dates when complete specimens were lacking, Gladwin said: "all that can be said for this is that it is a misguided attempt to endow tree-ring dating with an accuracy for which there can be no authority or excuse". If archaeological and tree-ring evidence are in conflict, he would always rely upon the archaeological.

The pendulum of climatic investigations has likewise swung from one extreme to the other. All the trees of a region record the lean and the fat years (Davis, 1931); naturally we would like very much to know how and why. The idea that growth is largely dependent upon annual precipitation came as an inspiration (Hawley, 1939). To many people a 500-year record of weather derived from tree rings was not only astounding but "smacked of witchcraft" (Abbott, 1946), and the evidence of weather contained therein was as irrefutable as fingerprints. A simple statement, however, that a thin ring means a dry year and a thick one a wet year is perhaps a bit over-simplified (King, 1951). "The relations between growth and climate are . . . perhaps not always as direct as we are often apt to believe" (Hustich, 1949). Weather undoubtedly influences tree growth, but our ability to analyze that growth may not as yet permit us to read an "accurate history of weather for centuries past" (Science Digest, 1950). If growth can not as yet be analyzed with unfailing accuracy, it is somewhat premature to suggest that weather may be predicted for "decades, even centuries, into the future". This is especially interesting when we are told that ordinary methods of weather forecasting predict one or two days in advance, and then only with something like 50 per cent accuracy.

In contrast to the above statements, Friesner (1943*b*) frankly pointed out that "there still remain today a number of unsolved problems" having to do with the relation of climate to tree growth. Hustich (1948*a*) discussed annual alternations of various types of growth dependent upon climate: "We must, however, have a deeper knowledge of the physiological processes in the shoot development and of the awakening of the cambial activity to understand the true relations between climate and growth". A year later he said that no correlation existed between tree-ring series in Alaska and in Scandinavia or even between series in continental

Lapland and on the coast of Norway because they are in different climatic regions: "In this respect the importance of dendrochronology has been highly overestimated". A more hopeful note is sounded by Brier (1948): ". . . it seems appropriate to endorse the closing remarks of Jones (1947) to the effect that the investigation of trends of growth shown by trees over long periods (as distinct from the attempts to interpret the peculiarities of individual rings—Jones) offers a promising field of work for the climatologist studying long-period fluctuations in the world's climate".

Thus claims have been made both in chronology and in climate that are somewhat extreme. Words of caution have appeared from time to time. But our greatest concern is not with the extravagance of the claims in themselves, claims encompassing accurate dating to the year of tree growth 19 centuries in the past and substitution of tree-ring thicknesses for weather records not only centuries in the past but also centuries in the future. Our concern is rather with the suggestion of final accomplishment and dogmatism in certain methods, in mathematically restricted statements and in sharply delimited classifications which, if unchallenged, would reduce further inquiry in several fields to mere routine and blight the spirit of research in student and experienced investigator alike. In any event, be the claims valid or not, we may perhaps be forgiven if we prefer the zest of uncertainty and discovery among the biological variables inherent in tree growth rather than case-hardened finality in our results.

GROWTH AND GROWTH FACTORS

THE FACTOR COMPLEX

Botanists for years have realized full well the highly complex array of factors which influence tree growth (i.e., Brown, 1915; MacDougal, 1923), and some have done detailed experimentation with one factor alone, e.g., soil moisture (Veihmeyer, 1927). Such realization and experimentation have given us a clearer overall picture of the problems of tree growth than a host of correlations between growth and a single factor. More and more, however, all workers have become impressed with the multiplicity of factors, the complexity of their inter-actions, and their detailed areal variability.

The statement of Daubenmire (1948–49) may fit the problem of growth factors: "It is clear that no one factor can be used to ex-

plain all variations in the phenology of all plants. It also seems safe to state that, although certain general principles may apply to many plant species, deductive inference will never permit accurate prediction of the ecologic relations of particular species that have not yet been the object of special study". And for such study the fundamental work of Pearson (1950) over many years must point the way. The analysis of climate alone is, according to Brooks and Kelly (1951), a very complex task, and no less complex is the study of vegetation and soils because they are "mirrors of the normal climate of a region" (Hare, 1951). In the words of Watt (1943) there is "need for a dynamic conception of forest ecology. The pattern of the forest plantation must be determined by a variety of causes: microclimates, soils, relations between one plant and another, and the structure of the vegetation; the organic factors of the environment being no less important than the inorganic". It is conceivable that secular trends in radial increments can be brought about by release of one kind or another, by reduction of crown, by periodic pest attacks, by fruiting or by variations in competition. Shirley (1945) reviewed the problems of light as an ecological factor. His study "further emphasizes the desirability of seeking through factorial design of experiments and multiple correlation analysis, to work out the true interrelationship of the several growth factors of plant habitats. To confound them with one another inevitably confuses thinking, thereby adding mystery to subjects open to clear analysis".

Many workers call attention to the multiplicity of factors; a single phrase in each case illustrates this: "complexity of the processes concerned with the water relations of plants" (Broyer, 1951*b*); "complexus of factors concerned with . . . water movement into plant systems" (Broyer, 1951*a*); "width of rings . . . determined by a complex of interacting factors" (Gladwin, 1940*a*); "it is . . . readily seen that diametral increase is not controlled by any one factor of the environment, but by a combination of factors" (Friesner, 1941); "for the thickness (of tree rings in the climate of Potsdam, Germany) depends on a number of factors often independent of climate" (Meissner, 1943); no one factor controls fruit production, "rather a complex of factors" (Pearsall, 1950); "apparently so many factors having an important bearing on the total growth (of coast redwood) that correlation with any one of them

is not feasible" (Schulman, 1940*a*); "tree growth depends on many factors" (Hawley, 1941); and "growth of young trees depends upon a complex of factors" (Vegher, 1946). Kramer (1948) goes a step farther and relates tree growth not only to environment but also to heredity.

The difficulties of observing all factors at the same time or even of measuring more than one are rather great. However, such attempts have been made by Gustafson (1943), Hustich (1948*a*) and Kaufman (1945).

In relation to growth and growth layers specifically, the views of several workers should be given. Turner (1936*b*), who worked in Arkansas, emphasized the role of soil and topographic features, not neglecting the "possible effects of differences in the climatic complex" on height growth. The rate of such growth, however, "cannot be correlated with any single factor, but rather is dependent on the interaction of several factors".

Friesner and Friesner (1941) recognized the importance of all factors on the formation of annual rings. Although some factors are internal and hereditary, whereas others are external and environmental, "variations in growth . . . from year to year within the same individual are related more definitely to environmental than to internal factors". Temperature and light among the external factors are commonly adequate for growth, and available water commonly is the limiting factor. Thus "growth curves of trees will more often show a relation to rainfall curves than to those for any other single factor". But rainfall used alone has its problems because "the relation of growth curves to rainfall is not a simple one. Such factors as the following enter to make the relation complex: the time of year when the rains come, the proportion which comes during the growing season, how well they are distributed over the growing season, the topography and its relation to runoff, the character of the soil and its ability to store water from times of abundant to times of inadequate rainfall". The storage of water depends upon climate, depth and nature of the water table, and the local geology, in relation to the root habits of the trees concerned. It may be more a matter of food manufacture and storage than of water holdover. Later, in 1950, Friesner stated that he is "dealing with a complex of variables and the degree of relationship of any one of them with growth will be modified by the others".

Hanson in 1938 fully recognized the factor complex. In addition to climate, he found that disease, insects, animals, fire, lightning and competition have an influence on growth: "Thus it is not always prudent to base small annual rings or variations upon climatic conditions". He further emphasized the complexity, in 1941, and discussed even more factors, but, since "climate is probably the most unstable factor of the environment, it is only natural to expect some correlation between climatic fluctuations and tree growth". There are, nevertheless, many characteristics of rainfall and soil which in part determine the amount of soil moisture present when trees need it. Therefore "it is apparent that the total rainfall in an area is not necessarily an index to the amount available for tree growth".

In a review appearing in 1941 Pearson remarked that "the erratic behavior of growth curves in relation to climatic records is well known to foresters and ecologists in this country who have attempted such correlations". Pearson himself kept records in the midst of the trees he studied and repeatedly (1950) emphasized the multiple nature of growth factors. A striking contrast to the remarks of Pearson appeared in the statements by Lyon (1949) who worked in New England. He points "to the accumulation of considerable evidence that the secondary growth of many conifers is determined to a large degree by the water supply available to their roots during the growing season". Therefore he offers the following: "When the annual growth increment does not agree well with the precipitation record, the relative ring width is a better index of the water supply available to the root system than are the records of weather bureau stations, due to the complexities of runoff, evaporation, interception by crowns and water holding properties of soils".

A close view of the work being done with growth layers nourishes the hope that fundamental investigations will more and more come to the front. Such experimental work as that of Blackman and Rutter (1950) on light and nutrients or that of Went (1949) on growth in an air-conditioned greenhouse points the way to us in growth-layer studies. "In the field the plant is never subjected to a single variable" (Went, 1950).

Chowdhury, working with growth rings in India (1940), was not able to assign "growth activity to any particular factor". Millet (1944) studied the growth increments of Monterey pine in

Australia in relation to rainfall and concluded that "the problem of growth of a forest and climate will not be near to a satisfactory solution until much more of the environmental complex is taken into account". Working on hemlock, Meyer (1941) said that "it remains an unsolved question what meteorological factors or combination of factors influence the annual growth of trees in northern Pennsylvania, where rainfall is not a limiting factor". A very similar conclusion is stated by Friesner (1943*b*): "The problem of sorting out the different factors of the environment and determining just what role each plays in the matter of growth is well nigh unsolvable because the behavior of the individual is its response to its total environment". Byram and Doolittle (1950) worked on the growth of shortleaf pine of the South from the standpoint of silviculture; their remarks perhaps apply equally well to growth studies in general. In respect to radial growth they say that "it is not possible to designate specific factors as having dominant effects on tree growth. Several factors seem to share the leading role in regulating radial growth rate, and the position of most importance alternates from one factor to another". They therefore suggest a possible remedy: "The progress of silviculture and forest management will probably be greatly accelerated when there is more basic knowledge on the physiology and chemistry of the individual tree and the components of its environment. To understand the tree as an individual may be the most important step in ultimately understanding and predicting its behavior in a stand". Such surely must also apply to problems of ordinary annual growth. Lutz (1945) apparently agrees, for he wrote: "To the reviewer the need for experimental investigation of the relations between width of tree rings and climate, soil, and competition seems particularly urgent. In other words, we need more precise information on the relation of diameter growth of trees as influenced by environmental conditions. With information of this character available the possibilities of dendrochronology will be very great indeed". The lack of experimental and observational work on tree growth has also been emphasized by Glock (1942a).

FACTORS AT A PARTICULAR SITE

FUNDAMENTALS. During the past decade botanists have continued their fruitful studies of individual growth factors in relation to growth, on the one hand, and to the multiplicity of factors, on

the other. Many studies illuminate the path of future investigations and at the same time neither obscure nor obstruct the biological complexity of the problems involved. In citing a few examples there is no intention of emphasizing their merits over many others: the calculation of growth in relation to age and vigor of pine, by Briegleb (1945); the stem analyses of Burns and Irwin (1942); the detailed growth of a single pine for a year, by Byram and Doolittle (1950); the effects of defoliation, by Church (1949) and by Baker (1941); the speed downward of soil-moisture percolation, by Colman and Bodman (1944); the relation of stream flow to precipitation in a semi-arid drainage basin, by Cooperrider and distribution of rainfall, by Darrow (1943); the time and rate of Sykes (1938); the relation of ocotillo growth to the amount and radial growth at different altitudes in relation to variations of temperature and rainfall, by Daubenmire (1945–46); a comparison of growth characteristics in deciduous and evergreen trees, by Daubenmire and Deters (1947–48); the studies of elongation and diameter enlargement, by Friesner (1943*b*); growth measurements on leader, needle, cambium and root, by Kienholz (1934–35); the growth response of pine in bog and upland of humid New England, by Lyon (1949); the lucid analysis of the forest-tundra ecatone, by Marr (1948); the comprehensive and fundamental studies of ponderosa pine over the years, by Pearson (1950); axial and radial growth habits of deciduous trees in Indiana, by Reimer (1949); the analysis of growth factors in Arkansas, by Turner (1936*b*); diameter growth of Monterey pine in relation to rainfall intervals in Australia, by Fielding and Millett (1941); the microclimatic studies of rainfall, by Linsley and Kohler (1951*a*, *b*), and of temperature, by Shanks and Norris (1950); the detailed experimental work on soil moisture, by Veihmeyer (1927); and the specific time of growth, both axial and radial, in relation to measured soil moisture, by Watkins and de Forest (1941).

These examples illustrate the value of prolonged observation, detailed measurement and controlled experiment to the problems of growth and the factors which control that growth. Many, if not all, of these studies are fundamental; they are part of the groundwork which eventually will give us a better understanding of the physiology of growth and of the xylem increments set off by cambial activity.

In spite of close analysis of some one growth factor, botanists have seldom lost sight of the complex of interrelated factors. The effects of drought, temperature and sunshine can scarcely be separated, or those of drought and insect attacks, or of fruiting years and rainfall. However, an attempt has been made to meet the difficulties by using, for instance, controlled conditions or by experimenting with one or two factors while the others are near optimum. As a result we have today a far more lucid picture of growth than 20 years ago because of the painstaking studies of botanists, foresters and horticulturists. A reference to all such work would go far beyond the scope of the present report. We would, nevertheless, be remiss if we did not mention a few who have analyzed a single factor while cognizant of the entire complex. Among these there are the works of Briegleb (1945, 1950), Byram and Doolittle (1950), Friesner (1941, 1943*a*, *b*, 1950), Friesner and Friesner (1941), Gladwin (1940*b*), Graves (1946), Hansen (1938, 1941), Huber (1948), Hursh (1948), Hustich (1948*a*), Marr (1948), Moseley (1941), Pearson (1950), Schulman (1945*b*), Shirley (1945) and Zeuner (1951*a*). Only under controlled conditions, guided by our experience, can we be reasonably certain of the exact effects on growth of the variations of some one factor. And we must be reasonably certain of our knowledge before we assign a single cause operating unobserved in the past to the production of a certain amount of xylem in contrast to an earlier or later amount.

LOCALIZATION OF FACTORS. The problems connected with growth in general or with discrete increments have been approached by two methods, the one having to do with the individual tree, the other with groups of trees. As regards the single tree in its highly localized environment, a relatively few studies in micro-ecology or microclimate give strong emphasis to a surprising amount of variation among many of the factors within short distances, both vertically and horizontally. Perhaps this, as well as internal differences, helps to explain why two trees which are separated by a few yards can respond somewhat differently in cambial activity and in the formation of xylem.

As regards groups of trees, many studies have been made in an attempt to measure or interpret growth response in relation to a factor general in its effect over the area. Two problems arise immediately. The first pertains to the universality of growth re-

sponse over an area. Some workers use practically all the trees, whereas others exercise high selectivity, even going so far as to reject by a two-fold process all except the slightest fraction of the entire stand. Selection, for instance, to avoid the effects of competition where the study of competition is not the desideratum, or to avoid a superfluity of repetitive data, may be entirely justified; but the rejection of trees, initially selected with care, because they do not conform to a subgroup within the larger group may give rise to serious questions. Which small subgroup out of a well-selected collection from a stand represents the growth factor being studied? Can we in the laboratory justifiably choose 10 to 20 per cent of the specimens out of a collection well-selected in the field and, because the growth-layer sequences have a certain type of similarity, hold that the small per cent records, say, the variations of rainfall? What do the other 80 to 90 per cent record? Which species records some one factor if each of two subgroups in a stand consists of one species conformable within itself but not conformable between the two? These questions are not rhetorical; they actually have come up in work with growth layers.

The second problem dealing with growth response concerns enlargement of the area. As the area of growth response expands, it is reasoned by some that factors operating locally lose their significance, and when hundreds of square miles are included, only an overall factor of most general effect exerts a uniform influence at widely separated time intervals. Such a factor might be the average temperature of the growing season, which could be sufficiently uniform over a large region to effect the growth of at least a portion of the trees a sufficient number of times during a century to permit correlation of those effects among the particular trees. However, even temperature fluctuates locally to a rather high degree, and the problem arises as to which trees represent the regional index and where they are to be found. Are they the trees whose growth responses measured by amount of wood formed are similar? And, if so, what are we to do with two or more sets of correlation from the same region? How can we as plant ecologists interpret the responses of the remaining trees? Since responses in respect to the amount of xylem formed can vary only in a three-way fashion—alike, unlike, or neutral—the results of chance correspondence must be eliminated from the measurements. The

value of finding a regionally integrated temperature gauge, or the like, is so great that no effort should be spared to carry on the work. At the moment the picture is none too bright, and methods employed should be critically examined by plant physiologists, ecologists and meteorologists.

An examination of the work done gives an idea of the trend of thinking. First perhaps we should examine what has been done about purely local factors, as in the area covered by one tree, and then pass on to individual factors over larger areas. Hursh (1948) used local climate in a slightly broader sense than many of us use microclimate. He measured air and soil temperature, wind, evaporation, air-moisture-saturation deficit and rainfall of three contrasted zones—bare, grassland, and grass and trees merging into forest in the Copper Basin of southeastern Tennessee. Two sets of three stations each crossed the zones, one set in a rough line less than eight miles long, the other in a line four miles long. Each zone, Hursh found, contained "a distinctive local climate", and each factor which he measured varied appreciably from one zone to another.

Shanks and Norris (1950) also worked in eastern Tennessee, on microclimatic variation in a small valley. They recorded temperature differences on north- and south-facing slopes, and the variability, seasonal trend, frost pattern and actual freezing damage at seedling level. Across the small valley the mean temperature differed by 3° F. The minimum temperature from ridge top to valley bottom differed by 6.4° F. There existed a difference of 20 days in date of the first killing frost. Thus differences do exist within short distances, differences that can affect growth.

In 1946 Ives wrote about diurnal air circulation in valleys in relation to the difference in altitudinal ranges of various species from valley to valley. Much of the variation remained unaccounted for, even after corrections were made for gross climatic conditions, effective daylight, available soil moisture and soil chemistry. This work of Ives illustrates another complexity that is local and can conceivably cause differences in neighboring trees.

Observations at Neotoma, a small valley in central Ohio, by Wolfe, Wareham and Scofield (1949), revealed great differences of temperature within one mile. In a frost pocket of the valley the minimum temperature on a certain day was —25° F., whereas

within a mile in the nearby woods beneath leaf litter the temperature was 29.5° F., a difference of 54.5°. Such a variation resembles that of tens of degrees of latitude or thousands of feet of altitude.

As described by Parry (1951), a thin hot layer of air heated by the sun lies close to the ground where it is bare. Where vegetation exists, the heated layer rises " to a height which depends upon the height and density of the vegetation ". Is it possible that such temperature differences could have an effect on physiological processes at different elevations in a tree?

Linsley and Kohler set up a network of 55 rainfall stations two miles apart to measure variations of rainfall during one storm (1951*b*) and during two intervals, April 29–September 21, 1947, and February 5–September 22, 1948 (1951*a*). The network was in the form of a rectangle five stations in width and 11 in length. In one storm of heavy rainfall from August 4 to 7, 1947, there was a high degree of variability ranging from about 0.2 inch to 3.4 inches. Neighboring gauges differed by as much as a factor of three. Over the longer intervals of time, areal variations in rainfall, although present, were relatively less than for a single storm. One line of gauges, each two miles from the other, gave readings in inches as follows: 43.2, 47.4, 50.9, 44.9, 51.4, 46.1, 55.8. Two other sets of two, two miles apart, gave 46.2, 53.0 and 47.2, 55.5 inches. In spite of these variations " extremely dense networks are not required if the occurrence of an occasional large error is not serious . . . a relatively sparse network can be utilized to determine regional precipitation characteristics ".

With respect to tree growth these highly local variations, as in rainfall, may account for the differences not only between adjacent trees but also between groups of trees. Variations in one factor, furthermore, added to those of other factors, create a complex situation which, it would seem, can be resolved only by detailed micro-ecologic studies. Then we may understand why the relative and absolute amounts of xylem formed in two adjacent trees resemble each other or differ, or why two trees remote from each other correlate and two close together do not. Statistical manipulation appears to have been called upon occasionally in order to attempt elimination of certain growth irregularities. Perhaps Schulman (1951) has actually removed a portion of the influence

of micro-ecologic factors in partly removing what he calls the random term in growth of each tree by elimination of age trends. Environmental and genetic influences aside, can we have such a thing as a random term in tree growth? Giddings (1941) made an interesting comment about what may be construed as local factors when he said: "A long ring record carries enough dating characters common to the whole area to overcome misleading local aberrations".

RAINFALL. The unintentional confusion resulting from use of the word "climate" rather than some one element thereof has largely disappeared. A few cases do exist (Giddings, 1941; Hawley, 1941; Schulman, 1942*a*, 1945*b*, 1951), probably because of the desire to obtain variety in words. However, it is confusing and may be misleading to read the word "climate" and find that rainfall, or temperature, or some other factor is actually intended. One does not wish to read into a statement something not intended. For instance, heredity and environment, which cannot be clearly separated in nature, "govern the significance of ring-width series as climatic records" (Schulman, 1945*b*).

Students have come to "realize the difficulties of designating a single environmental factor as chiefly controlling one or all growth responses" (Sampson and Glock, 1942). Substitution of growth-layer thicknesses for rainfall records is no doubt an ambition of ideal proportions, but as yet there is no substitute for the standard method of emphasizing one variable while holding the others constant or, in the case of individual trees, selecting them so that the other factors have nearly the same impact on each tree. A majority of the workers in growth layers do emphasize one or more factors while at the same time recognizing the actual multiplicity of factors.

Because of the importance of water in our economy, it is only natural to seek all possible information on rainfall. Briegleb (1950) noted that wide periodic variations in rainfall and corresponding variations in tree growth characterize the ponderosa pine type. Although he emphasized rainfall, he was "aware that the rate of growth that occurs on a given site may vary widely, depending upon the genetic characters of the growing stock". Vigor, crown size and site have great influence on growth. During unfavorable periods low-vigor trees experience a greater reduction in growth

than do high-vigor trees. Among trees with good crown-vigor it is the older age classes which have the greater relative decline in growth. Trees on poor sites react to precipitation cycles by variations of increment in a more pronounced fashion than do those on good sites. Thus it is patent from the work of Briegleb and other foresters that more or less violent fluctuations in growth increment are to be obtained from low-vigor trees of younger ages, from good crown trees of older ages, and from trees on poor sites. Even so, growth also depends upon the genetic character of the stock. These low-vigor poor site trees yield growth-layer sequences designated as variable by botanists and foresters and as sensitive by several of the tree-ring workers. The one term is descriptive, the other interpretative. Physiological investigations on growth and growth factors will in time indicate whether or not the selection of the term " sensitive " was a happy one.

Rainfall and temperature are treated as mutually interacting factors by Byram and Doolittle (1950) in their study of the Southern shortleaf pine, although they maintain in general that " it is not possible to designate specific factors as having dominant effects on tree growth ". During the spring, growth was at a maximum when light, moisture and temperature were at an optimum; limiting effects may have been exerted by available nutrients, or by inherent characteristics of the trees, or on warm sunny days by a transpiration rate greater than the vertical transport of water, even with an excess of soil moisture. Stored soil moisture decreased in June, and from then until August soil moisture was a limiting factor on radial growth. Prolonged drought induced shrinkage of tissues, and " the length of time for recovery following a rain seems to be determined only by the time required for the water to reach the roots ". This study by Byram and Doolittle of a year of detailed growth in the life of a single shortleaf pine may serve perhaps in its biological approach as a decided contrast to other studies with a mathematical approach.

In a very straightforward fashion Dale (1947) described the hot winds and the uncertainty of rainfall on the Great Plains which, after all, are similar to a lower forest border except that climatic conditions are more extreme and fluctuations more violent. Darrow (1943) studied the growth of ocotillo and found that " the amount and frequency of terminal branch increment vary with climatic

conditions and with the general age of the individual plant or branch". Vegetative increments depended upon amount and distribution of precipitation. As a rule, terminal growth occurred during the summer rainy season and only occasionally in spring. The size of the branch increments likewise seemed to depend more upon the amount of summer rainfall than upon that of spring. A very low summer rainfall after a moderate spring rainfall gave a minimum of active branches and a minimum amount of growth.

In southwestern England Dobbs (1942) studied ring patterns in larch which is rarely subjected to a condition of limited moisture. This is modified somewhat, however, by the conclusion that "the number of false rings appears to vary inversely with soil depth". Certain narrow rings did correspond to drought years, but on the whole even trees on the same site failed to give a uniform pattern of growth. Under the conditions in southwestern England many local patterns existed in conjunction with certain regional similarities. It will be interesting to learn how well growth-layer thicknesses correspond to rainfall in view of local differences and regional similarities.

Douglass (1945, 1946*b*) strongly emphasized the role of precipitation in the southwestern United States, although, as will be seen later, he relied strongly upon steep slopes and thin to patchy soils as controls for tree selection. Thus lower forest border conditions were highly accentuated and even completely atypical in so far as moisture conditions on a normal site were concerned. This insistence on atypical factors at a particular site should be contrasted with the work of Lyon (1943, 1949), Friesner and his coworkers (1941, 1950, etc.), Dobbs (1942), Glock (1950) and others who found correspondence between rainfall and tree growth, not in the extreme lower forest border but in the forest interior. Douglass (1946*b*) in photographs contrasted complacent and sensitive ring records: "In our dry country, complacent ring sequences . . . indicate that the tree is getting sufficient water and does not respond to changes from year to year". Would this lack of change, then, indicate that all growth factors are in perfect balance and near optimum in relation to each other year after year? The botanical and ecological implications of the quotation bear so many facets, aside from the terminology used and the principles of geographic distribution of species, that a complete discussion is im-

practical. If the ring sequence actually is completely uniform ("complacent"), then the tree must have had an optimum amount of water, never too much, never too little, for uniform yearly growth—constant water supply and no long-continued submergence of all roots. Such a site would, in our experience, be atypical to the ponderosa pine zone. Drought in humid regions affects the trees native to the region just as it does trees native to dry regions. Such instances were the death of beech during drought in Ohio and defoliation of trees in the District of Columbia during a hot dry spell. The capacity of trees to respond to changes of one kind or another in the environmental complex can hardly be expected to be confined to the trees growing along the edge of the desert in the Southwest.

In Australia Fielding and Millett (1941) studied diameter growth of Monterey pine by means of the dendrometer under two different climates, the one a dry upland with irregular rains and the other a more favorable forest climate with seasonal rains. Distinct diameter growth in the dry upland occurred only during spring; but growth always followed soaking rains of summer and autumn. Under the forest climate there were two main periods of growth, spring and autumn.

Friesner (1950) studied the effect of rainfall on six species of hardwoods in Brown County, Indiana, and concluded that the particular site played an important part in the relation of a tree to rainfall. In 1941 Friesner and Friesner had studied the relation of ring growth to rainfall in six species of hardwoods from Marshall County, Indiana, and found that during the normal growing season available water became the limiting factor while temperature and light were commonly adequate. The bare rainfall figures for any single interval did not always correspond closely to growth—the condition of the soil, the amount of runoff, and the nature and amount of rainfall in the months preceding the growing season were modifying factors.

Giddings (1941), working in Alaska, held that trees reflect climate if the relative thicknesses of the respective growth layers correspond from tree to tree. This visual correspondence was called "crossdating". Later Giddings restricted the climatic control to that of temperature. Complacent sequences mixed in with sensitive were difficult to explain on a temperature basis. Because

the river-bottom trees agreed among themselves but varied from the record at timberline, Giddings interpreted the difference as a disturbance due to local conditions of slope, stream action and ground cover. If temperature is a major factor in the Northlands, and it seems reasonable, we wonder what a detailed study of temperature stratification, temperature inversion and altitudinal effects would show.

Rainfall records, in contrast with those for soil moisture, for instance, are comparatively easy to gather. What trees, from what zone, growing under what conditions record rainfall to the greatest extent? Glock (1950) took his trees from the forest interior—upper part of transition zone in northern New Mexico—and related growth to rainfall. Hansen (1941) related growth to rainfall in trees from near the lower forest border in central Washington where " precipitation is probably the chief limiting factor in the growth of trees . . . and the nearness of the timberless zone indicates the presence of unfavorable conditions ". Thus conditions are below optimum especially as regards temperature and rainfall: " It is apparent that the total rainfall in an area is not necessarily an index to the amount available for tree growth, of which radial increment is a function. The time, the amount, intensity, type, and frequency of precipitation, in conjunction with the depth, porosity, water holding capacity, and structure of the soil, and the topography, control the amount of water retained. Once the water is in the soil, the temperature, the H-ion concentration, structure, and texture of the soil further control the amount of water available for absorption by the plant ". This summarizes at least partially the extent of the problem that concerns ecologic factors at a particular site and perhaps should be compared with the statement of Hawley (1941) that for her purposes in a large area centering in Tennessee it is sufficient to know a tree's location within 50 miles: " The tree-ring areas have been found to be so large that this approximation of location is close enough for all the work except that of special botanical and ecologic interest in giving the exact reaction of a tree to its surroundings . . . since the major interest of the laboratory so far has been cross-dating trees and extending charts, the data regarding geography and location within the fifty mile radius has been sufficient ". Although these statements have been criticized by Glock (1942*a*, *b*), they should be compared, first, to the work of

Lyon (1943) who found areas of homogeneous growth to be much more restricted in New England than Hawley did in the eastern part of the Mississippi drainage basin, and should be compared, second, by the individual botanist with his own ecologic work. Miss Hawley studied trees grown under a rather humid climate and related their growth to rainfall and temperature.

Kapteyn (1914) in western Europe and Lyon (1943) in New England considered water supply as governed by rainfall to be the dominant factor in tree growth. Apparently trees growing at the edge of the desert are not alone in recording rainfall. Although Lyon found growth resemblances in extreme years up to a distance of 50 miles, he said that "The fluctuations in the values of the mean ring widths from year to year are . . . due to environmental factors at the site, chiefly those of climate because the edaphic factors are fairly steady in a forest in relation to the dominant climate". In an interesting comparison of bog and upland pine in New England, Lyon (1949) found that in their growth on the two sites the trees had strong similarity to each other, contrary to what one would expect. Rainfall combined with release is the factor of greatest influence on both upland and bog trees.

High temperature combined with moisture deficiency killed feeding roots of jack pine (MacAloney, 1944) and brought on severe decadence. Even though budworm defoliation did not directly cause death, it helped in the final stages: "The death of the trees was very probably due, in the final analysis, to the drought in 1938 and 1939", which terminated 20 years of drought or near drought. But it should be noted that under the drought conditions only the poorest trees decreased their growth in basal area, whereas the best trees increased their growth.

Pearson (1950) has given us a fundamental analysis of the effect of site factors on the growth of ponderosa pine in the southwestern part of the United States; in fact his work is so fundamental that a deserved résumé of it would go far beyond the limits of available space. He emphasized the interacting complexity of growth factors —soil moisture, temperature, light, release, rooting and soil. Even so, "competition for the limited moisture supply dominates the whole ecologic picture". What Pearson's work means to the forester and ecologist is illustrated perhaps by his attention to details affecting trees at particular sites. The opening of crown canopies

in dense groups at Fort Valley, Arizona, could increase the total precipitation reaching the ground by as much as 40 per cent. Such an event combined with the fact that " large trees as far as 200 feet apart may possibly send their roots into a common zone " gives us something to consider when we attempt to interpret the reasons for variation in xylem increment in the past; that is, growth variations may be caused by factors other than climate or climatic cycles.

In a series of papers Schulman (1940*a*, 1942*a*, 1943, 1945*a*, *b*, 1947*a*, 1951, 1951–52*a*) stressed the relation of growth to rainfall in saying that trees act as natural gauges of annual rainfall (1945*a*) if they grow under extreme conditions of the lower forest border. Extreme emphasis on the water factor served, it seems, to mask the effect of other factors. The habit of selecting trees whose water relationships were abnormal has been carried over to Arkansas (1942*a*), but discrepancies between growth and rainfall crept in and were caused by disturbing factors. Although rainfall was emphasized by Schulman, he tested for temperature relations and recognized many of the physical problems connected with a complex of factors.

Weakley (1943) in western Nebraska gave his attention wholly to the rainfall-tree growth relationship among softwoods which grew well above the dry washes.

TEMPERATURE. For some reason students who work with growth increments pay less attention to temperature effects or have less success with them than with rainfall. Precipitation is measured from interval to interval, but temperature is taken for the most part as minimum or maximum. If perhaps the amount of temperature (or heat) could be measured quantitatively from the time growth begins until it ends (and these dates vary from tree to tree), we might have better success in relating specific tree growth to temperature. Some references to temperature have already been made; for the most part, workers who consider temperature do so in conjunction with other factors.

Daubenmire (1945–46) measured radial growth of trees at various altitudes in Idaho by dendrometer and found growth related to the interaction of temperature and soil moisture modified by altitude. High temperature aided growth if soil moisture was available. In a later study, Daubenmire and Deters (1947–48)

measured the growth of deciduous and evergreen trees at Moscow, Idaho. No tree was native, but all had become adjusted. Of major interest to them were the relationships of temperature, soil moisture and soil temperature to growth. Although dendrometers may not give us a perfect record of growth, the basic work of Daubenmire and Deters does seem to cast a measure of light on certain growth characteristics.

The same may be said for the work of Friesner (1941, 1943*a*) who studied growth in the beech of Indiana by the dendrographic method (1941). He related growth chiefly to temperature and soil moisture but discussed other factors as well: "The most important external factors controlling wood formation which are variable on the same site from season to season and day to day are temperature, evaporation rate, and available water". Probably temperature was a limiting factor early in the season when water was available and water became limiting later when temperature was adequate: "The relation of these factors is not a simple one . . .". Friesner's study of elongation (1943*a*) perhaps emphasized the role of temperature because the period of observation was shortened to a day or so. The present writer has daily observations of tip growth on fruit trees in Maryland. These showed a close correspondence between temperature and tip growth while tip growth was in active progress.

Giddings (1941) worked with trees in northern Alaska where water supply was adequate during the short growing season. Growth took place during the longest days, days of greatest solar energy. Temperature and altitude had a fair relation to growth, a relationship which brought in complications because cambial division occurred at different times at different places in such a fashion that ring thicknesses did not match. If other factors such as altitude, soil moisture and soil could be held more or less constant, it might be that xylem increment would be found to correspond to some aspect of the temperature regime in air or soil during the interval of greatest physiological activity. Since a priori logic suggests that temperature is an important, or near dominant, factor at high altitudes and high latitudes, one hopes that Giddings and other high latitude students can resolve some of the complexities and thereby clarify the temperature relations, should such actually exist.

Studies on tree growth in northern Europe are perhaps well illustrated by the work of Hustich (1948*a*) in Finland where temperature appeared to be the factor of paramount importance, and great differences in altitude did not complicate growth reactions to the extent that they did in Alaska. Hustich, however, did not consider temperature exclusively; he found relationships with wind, light, flowering and fruiting. For instance, " The wind is . . . a climatic factor which in the polar regions is hard to distinguish from the low temperature ".

SOIL MOISTURE. Tree growth depends not so directly upon rainfall as upon the soil moisture present and available at the time when that growth can and does occur. Mr. C. K. Cooperrider, in conversation during a ride across the dry lands of southern New Mexico some years ago, mentioned the prime importance of the role of soil moisture in tree growth and suggested that students of growth increments would be striking closer to the heart of their problems if they measured the fluctuations of soil moisture instead of using rainfall records in tree-growth comparisons. No one can deny the importance of the suggestion. But rainfall records are, so to speak, ready-made for our use, whereas the collection of soil-moisture data entails laborious sampling at very short intervals over a period of years. We await the means and personnel for such a project. In the meantime we are aware of the acute desire to find a shortcut method for the revelation of meteorological records of the past in tree rings. Such desire has been shown by the following expressions: " indices of past winter rainfall " (Antevs, 1948); " accurate history of weather for centuries past " (Science Digest, 1950); " centuries-long histories of precipitation " (Schulman, 1943); " natural gauges in trees which have been continuously recording fluctuations in annual precipitation " (Schulman, 1945*a*); and " precipitation records from tree rings " (Will, 1946). In contrast, Friesner (1941) tells us that diameter changes reveal an immediate and close relation to available moisture, as shown by the irrigation experiments of MacDougal. The work of Friesner and MacDougal does not lend itself to such spectacular phrases as those listed above, but one feels that in the long run botanists and foresters will have more confidence in work of such caliber.

Much work has been done on soil moisture, per se, and inter-

related factors. Soil scientists have made great contributions as have also the men and committees whose work has been reported in the Transactions of the American Geophysical Union. Because so much work has been done it would be impractical to make a complete report; a few illustrations only will be given. He who would approach the problems of tree growth intelligently and understand some of the fundamentals underlying the growth layers which he uses, must know something not only about soil moisture but about the soils themselves. If and when facilities are available, tree growth must be studied in relation to soil moisture which in turn must be studied in relation to rainfall.

Colman (1944) studied field capacity in relation to depth of wetting. Field capacity, he said, was considered to have been reached two or three days after irrigation in well-drained soils of at least moderate permeability. In fact, any rapid changes in soil moisture must have occurred in the first 24 hours. Obviously the speed by which wetting occurs, field capacity is reached, and capillarity, evaporation and transpiration are carried on, helps to determine how much soil moisture is available for tree growth and for how long a time. This impinges directly upon food manufacture, food storage and so-called lag effects which are discussed by some students of tree rings where the thicknesses of two growth layers of the same date in different trees do not match or where a growth layer seems to match the rainfall of a previous year instead of that of the same year.

Information on downward wetting has been expanded by Colman and Bodman (1944) in their study of moist and layered soils by experimental wetting. In air-dry sandy loam, 12.5 centimeters of water penetrated 37 centimeters in 100 minutes. In initially moist soil, 6.7 centimeters of water penetrated 61 centimeters in 100 minutes. Water took about 400 minutes to penetrate 36 centimeters where 14 centimeters of sandy loam overlay silt loam. If the water penetrated to the silt loam faster than it could pass the silt loam, the excess ran down the plane of contact. Such factors at a particular site are not too easily visualized by inspection of the surface alone.

It may not be amiss to refer back to the thorough work of Cooperrider and Sykes (1938) on a semiarid drainage basin in the Salt River area of Arizona. One inch of rainfall commonly pene-

trated less than three inches into badly eroded soils bare of vegetation, whereas it reached six to eight inches or more on the same slope if covered by plants. The end of the winter rainy season and subsequent depletion of soil moisture came at the time when the full growing season was inaugurated. Much later, summer rains revived grasses and other kinds of plants, and even trees and shrubs with roots near the ground surface were under conditions favorable for growth.

In addition to the comprehensive summary on soil moisture in relation to plant growth by Kramer (1944) there are briefer, more specific reports. Kittredge (1949) measured rainfall in the open and under trees on 142 foggy days. In the open he obtained 25.19 inches rainfall, whereas under the trees he got 36.42 inches. Thus drip due to fog came to 11.23 inches which is an average of 0.08 inch per day. Schiff and Dreibelbis (1949) measured rate and depth of infiltration of soil moisture in eastern Ohio. For the topsoil or plow layer they found a maximum penetration of ten inches per hour and below that 0.6 inch per hour.

A person concerned with forest ecology finds it necessary to refer back to the significant experiments on soil moisture by Veihmeyer (1927), experiments which bear directly on problems of tree growth. For instance, irrigation in the dormant season did not postpone to any great extent the time in the following season during which the supply of moisture in the upper six feet of soil was reduced below the wilting coefficient. Such a conclusion surely must be taken into account when we seek to correlate tree growth with precipitation which falls prior to the start of the actual growing season. Or again, the growth of trees was not influenced by fluctuations of water supply as long as it fluctuated below maximum field capacity and above the wilting coefficient. Irrigation water moved laterally only to a slight extent. Such conclusions bear directly on the study of tree growth from the forest interior; we must seek for the reasons for growth variations elsewhere than in a mere single relation to amount of rainfall.

Oosting and Kramer (1946) found that light and soil moisture were almost equally important in the survival of conifer seedlings on the Piedmont Plateau. Two of their observations were: *a*) trenching gave better survival and indicated that it depended upon competition of roots for soil moisture; *b*) seedlings did get estab-

lished successfully at the edge of openings where soil moisture equalled that of the forest interior but light was better: " Thus, the pines at the margin, which are probably able to manufacture more food and therefore to develop more extensive root systems, can survive drought better than those in the forest. . . . light is probably more significantly controlling than soil moisture in the complex of factors limiting the establishment of shortleaf pine (and loblolly) seedlings under forest stands ".

Many of us feel that Pearson (1950) of the Southwestern Forest and Range Experiment Station understood the ponderosa pine of the Southwest better than anyone else. He impressed upon us constantly the complicated nature of the growth processes and the complex impact of the many growth factors. Soil moisture, temperature, light, wind, competition, release, soils, rooting, damage by squirrels, mistletoe, and the like came under his attention in his study of ponderosa pine: " From seed to sawlog its growth, form, and existence are governed by heat, light, and moisture. . . . Competition for the limited moisture supply dominates the whole ecological picture . . . . Response to release from competition is as universal as competition itself . . .". In his study of light requirements Pearson observed trees in the open and under 50 per cent, 67 per cent and 85 per cent shade. Increasing shade drastically reduced basal diameter and height growth. Small wonder that Pearson expressed to us his distress with the hasty attempts to find a simple one-to-one relation between tree growth and a single factor such as rainfall whose course must trace a devious route, in balance and unbalance among many other factors, through soil, root and stem, and through physiological changes before it can influence the amount of xylem in an increment. Pearson, none the less, emphasized the importance of soil moisture in the Southwest, for " In regions of deficient precipitation, space requirement is primarily an expression of water requirement, although light also plays a part . . . ". Those of us who work with tree growth owe a great debt to Pearson for his report of 1950—we wish we could detail all of the guiding experiments he performed.

Studies by others have been important, even though not so comprehensive as those of Pearson. In North Dakota Will (1946) emphasized the importance of moisture " available to the roots in

the year in which each ring is formed". In California Watkins and de Forest (1941) detailed the time of growth of some chaparral shrubs dependent upon soil moisture. In Colorado Williams and Holch (1946) studied the zonation into pine, scrub oak and grass, and ascribed this zonation to "the difference in soil texture of the three habitats, together with its effect upon the hygroscopic coefficient, and the resulting quantities of water available to the plants".

SOIL. Soil without moisture is of no use to plants; with moisture it immediately becomes an active portion of the total environment, chemically and physically, as the single factors alter their mutual relationships. Here, as in the study of other factors, soil as a factor is emphasized but not treated to the exclusion of others. Billings (1950) found patches of ponderosa and Jeffrey pine in the zones occupied by sage and piñon-juniper, at lower elevations under much less rainfall than the normal ponderosa pine zone of the Sierra Nevada. Such islands of pine resisted the invasion of sagebrush because of mineral-deficient soils on hillsides and ridge tops. In east Texas Chandler, Schoen and Anderson (1943) decided that, of all factors studied, soil type proved to be the best indicator of site quality of loblolly and shortleaf pine.

Marr (1948), in his work on the east coast of Hudson Bay, excellently combined a knowledge of ecology and growth-ring analysis. Soil in a broad sense controlled tree distribution; it had no relation to exposure. A considerable diversity of form was related to variations in the type of soil. Growth factors may be grouped as atmospheric, edaphic and biotic, and it is possible to emphasize the effects of the first by proper selection. However, "At the present stage in growth ring research it is not possible to relate ring characters to any one environmental factor".

Minckler (1943), working in Tennessee, studied the effect of rainfall and site factors on the growth of six species of trees including two pines. Soil-rainfall relationships were complex; the nature of the "B soil horizon" affected the "growth of all species tested except shortleaf pine, and the effect of reduced rainfall is much greater as the impervious quality of the B horizon increases". In a general way, exposure also influenced growth. All species made better growth on sites with deeper topsoil. Oddly enough, shortleaf pine was not affected by seasonal rainfall, soil consistency,

aspect or depth of A horizon. Growth was remarkably uniform except with dense vegetative competition.

Paul and Smith (1950) related growth to type of soil and nature of topography. The more impermeable the soil and the steeper the slope, the greater the runoff and the less water there was available to the roots of the trees. In an interesting article Roberts (1939) portrayed a simple and direct relation between depth of surface soil and average height of trees. Soil one inch deep had trees of 2.15 feet; five inches—3.65 feet; ten inches—5.41 feet; 20 inches—8.43 feet; 30 inches—10.83 feet; and 38 inches—12.16 feet.

In the Southwest Schulman (1945*b*) said the type of soil seems of little importance where it is extremely limited. This may sound unusual to soil scientists who realize the complex nature of soil genesis, evolution and profile. But soil was only one factor influencing ring widths in their use for "precise forecasting of climate", a feat beset by many difficulties, as Schulman emphasized: "Until the physical chain of events, seemingly existent, from variations in solar or other extraterrestrial phenomena to variations in sensitive tree growth is thoroughly explored and understood, this precise forecasting may, perhaps, not be made". Perhaps a biological and terrestrial chain of events would be of more intimate and immediate importance to an understanding of growth response in trees.

Storie and Wieslander (1948) studied timber sites at 163 field stations from the Pacific Ocean to the east side of the Sierra Nevada. In addition to the climatic factor there were four categories of soil factors: depth and texture, permeability, chemical character, and drainage and runoff properties. The sites for best growth of ponderosa pine, Storie and Wieslander found, need a deep soil (four to six feet or more) of sufficiently fine texture to hold about 12 per cent or more of soil moisture, a permeable profile, an absence of toxic chemicals, acidic reaction, well drained aspect, and an annual rainfall of more than 40 inches. Poor sites lay generally on the east flank of the Sierra where rainfall varied from 20 to 30 inches and the soil was shallow.

In the same region Stone, Went and Young (1950) studied another facet of the soil problem—the survival of Coulter and ponderosa pine on shallow soils that were often at the permanent wilting point for several months in late summer. Even so, these

two species apparently survive even though the soil is below the permanent wilting point. The cause is a different matter, for " this ability to survive on soils so dry that some plants die is yet to be explained ". Part of the answer, perhaps, involves what is called " negative transpiration " whereby aerial parts of the trees take up water from the atmosphere.

The work of Turner (1936*b*) has points in common with that of Minckler and Storie and Wieslander, especially as concerns soil analysis. Turner studied the growth of pine in Arkansas in respect to soil and topographic features. He classified sites into superior, intermediate and inferior, the last comprising extremely gravelly soils on rolling and hilly land, or soils with high sand content on hilly land, or very stony sandy loams with slope of 7 to 25 per cent. In contrast best growth occurred " on soils that are immature, flat, of high silt or silty sand content, with permeable subsoil and hence at least fair drainage but with obviously adequate water supply ". It is worth mentioning that Turner sampled the soils at three or four levels to a depth of 3.5 feet in order to determine, among other things, the physical structure of the A1, A2 and B horizons. In a later report Turner (1937) emphasized the poor quality of the site for pine where mountain soils and steep slopes prevail.

A portion of Burns' work in New England (1944) is of special interest here. His studies on soil temperature and frost conditions in the soil as a plant habitat bear directly on growth initiation, the course of growth and the length of the season, all matters of importance where gross amounts of growth year after year are arbitrarily compared with a single growth factor fixed in time.

RELEASE. Release from competition, whether by natural or artificial means, commonly produces a change in amount of growth. Are we certain of our ability to distinguish a greater amount of growth over several years caused by release, from a greater amount caused by a series of, say, wet years? This is much the same problem as trying to distinguish the slight growth of a heavy seed year from that of a very dry or cold year.

Foresters have carried out many experiments on release from competition by cutting out a part of a stand. In nearly all cases growth has increased for a time in the remaining trees. Favorable growth response has been reported by the following, as examples:

Boggess and Lorenz (1949), working with loblolly pine in southern Illinois; Chaiken (1941), working with loblolly pine in North Carolina; Downs (1946), working with sugar maple, white oak and yellow-poplar in West Virginia and Virginia; Hough and Taylor (1946), working with Allegheny northern hardwoods; Krauch (1945), working with Douglas-fir in the Southwest; Krauch (1949*b*), working with ponderosa pine in central Arizona; Lyon (1949), working with white pine which grew in bogs in New England; Paul and Smith (1950), working with the several southern yellow pines; Pearson (1950), working with ponderosa pine of the Southwest; Roe (1947), working with ponderosa pine of the Northern Rockies; Steele (1948), working with Douglas-fir of the Pacific Northwest; and Zillgitt (1945), working with sugar maple in the upper Midwest. Thus it seems that increased growth following release from competition is a rather general response among trees.

Release by girdling certain trees in a stand has promoted growth in much the same fashion, as was demonstrated by Bull (1945) in girdling hardwoods among loblolly pine in Louisana, and by Cromie (1945) in the woodlands of Connecticut.

Fire serving to release parts of a stand also promotes growth. This has been shown by Bruce and Bickford (1950) for longleaf pine; by Chapman (1941) who observed the combined effects of fire with seed years and a hurricane in the longleaf pine of Louisiana; by Wakeley and Muntz (1947) also for longleaf pine in central Louisiana; and Weaver (1947) for ponderosa pine.

Badoux (1946) examined 2126 pines in Switzerland and found that ordinary light thinning had only slight influence on current wood production. He stressed the importance of crown surface upon rate of growth.

Burns and Irwin (1942), working with pines in New England, observed that wide spacing increased the increment. Between the dry weight of foliage and the volume of 1940, and between the surface area of needles and the volume of 1940, they noted high correlation.

Jensen (1940), studying hardwoods in New England, reported that thinning in general helped growth but that growth increase declined rather rapidly after the second year. However, the factors in the response were very complex, and thinning changed the

relationships among air and soil temperature, evaporation, wind movement and humidity.

Ponderosa pines in Idaho were thinned by cutting (Miles, 1945) and showed an initial period of rapid growth followed by a decline of relatively short duration, and then a decided upturn. Are we able to distinguish such growth surges produced by thinning from those produced by other factors? In past times, as today, natural thinning occurred by disease, storm and other types of induced mortality. The problems thus brought up are amplified by Gevorkiantz and Olsen (1950) who, working on upland balsam fir in the Lake States, said that " Degree of competition does not remain the same even within a relatively short period of time, such as one decade, except in very old stands or in stands where the density is already near the assumed normal ".

Pearson (1943) reported on 15 to 30 years of observation of 8000 ponderosa pines in the Southwest. Although release stimulated growth, " the growth of individual trees is determined more by space available for root expansion than by crown size ". A large soil mass from which to draw moisture is of greater importance than leaf area. In fact, " a relatively small leaf area will suffice for the essential photosynthetic processes ". The work of Pearson in 1944, having to do with cutting cycles in ponderosa pine, brings forth the suggestion that surges, or cycles, of growth amounts by natural thinnings might in some respects simulate surges due to fluctuations of climatic factors. Such cycles suggest themselves also in the work of Roe (1947) with ponderosa pine in the Bitterroot region of the northern Rockies. After thinnings of various intensities, measurements made at five-year intervals for 35 years showed increased growth at the second, fourth and sixth lustrums. Rainfall, April–August, increased at the second and the sixth interval measurements but not at the fourth. To Roe it seemed that growth rates were influenced more by stocking of the stands than by variations in growing season rainfall.

The summary work of Pearson in 1950 carries even more emphasis on the recurring sequence: natural mortality, release of survivors and greater growth, adjustment and growth decline. As an epitome of this Pearson said that " there is a tendency for casualties to come in surges ". Can we as ecologists be certain that we can distinguish growth layers made by release surges from those

made by alternating series of wet and dry growing seasons? Students of climate must consider this intriguing idea, well known in forestry, when they interpret growth layers formed centuries in the past.

Zillgitt (1944), working with sugar maple in the upper Middle West, found that light cutting increased the rate of diameter growth, more so as the diameter of the original tree increased up to 18 inches diameter breast high. Above this size the rate was nearly constant. Furthermore, " the ratio of diameter growth at any given level to the growth at diameter breast high was equal to the ratio of the diameter at that point to diameter breast high ".

As we review the work of foresters and botanists we become more and more impressed with the wealth of information available to those of us working in tree growth.

DEFOLIATION, TOPPING, PRUNING. Defoliation, whether by natural or artificial means, affects tree growth in a fashion nearly opposite to that of thinning. Removal of a portion of the photosynthetic apparatus from a tree may be expected to reduce the amount of food manufactured and thereby the amount of xylem produced. In the southern Appalachians, Barrett and Downs (1943) pruned white pine in order to determine the growth response: " About 30 per cent of the number of living whorls may be pruned without seriously reducing the growth rate ". Boggess (1950) tried repeated prunings of planted slash pine in Alabama in order to determine the effect on diameter and height growth. The trees were pruned one-quarter, one-half and three-quarters of the way up the stem. Both height and diameter growth were correspondingly decreased. In fact, " any drastic reduction in the leaf surface of a tree will cause reduced growth. In forest stands reduced leaf surface may result from defoliation by fire, insects, disease, or pruning by man ".

Paul and Smith (1950), in their work on southern yellow pine, employed both cutting and pruning. Partial cutting often caused a sudden increase in ring width. Instances have been recorded where diameter growth of 80 years was doubled in 20 years of released growth. In contrast, severe pruning of the crowns caused a reduction in width of growth rings and curtailed spring-wood growth more than summer wood.

Pruning is of course artificial defoliation. Baker (1941) studied

gypsy moth defoliation in New England. In general, defoliation preceded diameter decrease in the same years. The greater the degree of defoliation, the greater was the decrease. In the words of Baker, " Growth and defoliation data of four species of oaks and white pine show a direct correlation between percentage of defoliation and decline in radial increment ". Over a ten-year period one-third of the diameter growth was lost. This becomes even more important when one learns that " Rainfall measurements taken at nearby weather stations indicated generally a lack of relation between variations in precipitation and growth rate ".

In his interesting work of 1949 Church discussed defoliation in a very thorough fashion. Whether defoliation is natural—by insects, fire, disease, storm or other causes—or is artificial, it always results in decreased diameter growth, an effect which can be spread over a large area. Less food materials are produced and hence less xylem is made. Church discussed six different insects whose attacks " under favorable conditions . . . can build up to epidemic proportions and sweep disastrously through millions of acres of valuable timber ". The decrease in growth commonly matches the amount of defoliation. On the whole, the effects of defoliation are so similar, regardless of the cause, and the positive and negative responses in wood production are so complex that it would be difficult indeed to pin down the specific cause for growth-layer variations in the past if one suspected defoliation of any kind.

It seems, however, that a ground fire which scorched entirely the crowns of shortleaf pines in the southern Appalachians (Jemison, 1943*b*) had no effect on diameter growth—it proceeded at a normal rate. In contrast, Stone (1942) sampled both burned and unburned longleaf pine in Mississippi and found a decided reduction in growth. Trees smaller than six inches diameter breast high averaged 23 per cent less growth during the year following the fire, whereas larger trees averaged 19 per cent less. Normal radial growth was usually resumed the second year after the fire.

Wagner in 1949 made an instructive study of the Coulter pine in southern California. Because of sudden cold, such as the drop in temperature in January, 1944, after 11 days of abnormally high temperature, or because of drought prolonged late into the autumn, the tops of the conifers were killed. Such dying at the top gave a narrow growth layer the succeeding year.

Reduction in growth due to pests of various kinds is recognized by Schulman (1945*b*, 1947). Not only may there be sharply reduced growth but also there may result a "complete quiescence of cambial cell division for one or more seasons" (1945*b*). Such a statement regarding cambial activity must surely be meant for a single inspected locality of a tree—it would seem difficult to prove for the entire volume of a tree, bole, branches and roots.

Defoliation caused by late frost, insects or droughts frequently produced double or triple false rings in hardwood trees which therefore were of little value to Weakley (1943) for chronology building. In particular, hackberry trees "go into temporary dormancy at almost any time during the growing season when the moisture supply becomes too scant to support further active growth. The result is almost invariably a false ring which frequently cannot be distinguished from a true annual one". For his tree-ring record in western Nebraska, Weakley used red cedar and ponderosa pine, the cedar showing a greater tendency toward doubling than the pine. In contrast with the hardwoods, however, the double rings in cedar were diffuse and thus recognizable. One wonders, in view of the statements concerning double rings in hardwoods and softwoods, how certain Weakley was that no sharp double ring existed in the cedars or pines.

No better summary, perhaps, of the two opposites, release and defoliation, exists than that of Pearson (1950). Anything which interfered with the hydrostatic or photosynthetic systems reduced growth. Pearson listed rodents, insects, browsing animals, mistletoe and fungi. These damaging agents, 12 at least, reduced growth and made serious inroads on timber production in the Southwest. But it is in the fluctuations of growth, either by release or by defoliation, that our chief interest lies at present. These fluctuations may be local or widespread; they may be brief or prolonged. What, then, are the criteria by which such fluctuations can be distinguished from climatic effects? Sometimes the effects are quite similar, other times not (Sampson and Glock, 1942).

Various other factors have been described as influencing growth, but only a few can be mentioned here: the effect of insolation and exposure (Boyko, 1947); wind (Hopkins, 1939; Oosting, 1948); woodchuck droppings near trees (Wallihan, 1947); litter removal (Jemison, 1943*a*); and the combination of borer attacks and

drought (Secrest, MacAloney and Lorenz, 1941). Beal (1943) correlated tree growth with outbreaks of the Black Hills beetle and found that most outbreaks occurred during times of deficient precipitation. However, exceptions prove that " epidemics may also occur during years of ample rainfall when growth is favorable ". Loss of effective rainfall by interception (Hamilton and Rowe, 1950; Rowe and Hendrix, 1951) is difficult to evaluate where rain gauge records alone are available. According to Rowe and Hendrix, the average annual interception loss among second-growth ponderosa pine in California was 12 per cent. Throughfall, stem flow and interception loss were directly related to storm size.

ABNORMAL VERSUS NORMAL SITES. Curiously enough, two workers apparently insist upon using abnormal trees from abnormal sites, whereas botanists and foresters attempt to use normal trees from normal sites or else select trees in order to compare the effects of different sites. The first group seeks to reproduce a meteorological, or runoff, record of the past, whereas the second group seeks to understand the details of tree growth and its response to the various interacting factors of the environment.

Douglass (1941, 1942, 1945, 1946*a*, *b*) and Schulman (1942*a*, 1943, 1945*a*, *b*, 1947, 1951, 1951–52*a*) have repeatedly emphasized that accurate climatic (rainfall) records can be found only in abnormal trees from abnormal sites. Steep rocky slopes, with soil present in patches or in crevices, at the lower forest border in the Southwest give them trees with ideal climatic records. In 1948, Antevs had apparently come to approve the use of abnormal material. A knowledge of soil, soil moisture, groundwater and topography perhaps militates against the use of trees from abnormal sites. Douglass (1941, 1942) described Douglas-fir growing on the precipitous slopes of canyons in Mesa Verde National Park and said (1942) that the trees are thus compelled " to subsist on the precipitation that falls on their own area ". Such trees can record rainfall of their immediate area only if the runoff downslope to the trees equals the runoff downslope away from the trees. If the trees give a record of rainfall, they do so in spite of the steep slope, not because of it. Because the principles underlying the relation of topography to groundwater penetration and its subsequent percolation are much the same over the face of the earth, it is of interest to read that " people who live in moist climates have great difficulty in

judging these topographic characters" (Douglass, 1941); or that specimens should be taken "in the field by someone who understands the effects of topography" (Douglass, 1941). Surely plant ecologists and geologists understand the effects of topography, and in addition they realize vividly that the amount of water penetrating the soil on a steep slope or the soil in pockets does not necessarily represent accurately the amount of rain falling on a particular part of the slope. On a steep slope runoff may not only bring water to a tree, but may also carry it away. Douglass said (1946*a*) that trees growing on high isolated points or in a crack in a rock are thoroughly protected from any imported water. True; but they are not protected from water exported before they have a chance to use it.

Schulman likewise emphasized selection of trees from adverse sites. Very dry sites in the Rocky Mountain region are "often characterized by open and scraggly but over-age stands" (1943). Great longevity accompanies great hardship. Samples are preferred from a tree growing "on a rocky southeast-facing lower slope of some 30° or less" (1943); or from a "steep open site . . . on a dry ridge-back".

In the Pacific Northwest, "Trees were selected (for core samples) on steep slopes and ridges bordering the coulee floors and at the dry lower forest limit" (Schulman, 1945*a*).

Single cores were taken from ponderosa pine and Douglas-fir scattered over the Colorado River basin (Schulman, 1945*b*): ". . . all sites represent well-drained slopes or ridges with thin soils and are near or at the lower forest border, where drought stresses are important". No wonder the trees "eke out a precarious livelihood". This being true, it is a bit difficult to agree that "The general advantage of marginal regions as source areas for dendrochronologic material seems obvious". Douglas-fir, a dry-site, slow-growing type, is said to be the best tree for chronologic purposes. Its normal site is on steep dry slopes. This must be compared to the statement of Preston (1940), the forester, wherein he says the Douglas-fir is "adapted to variety of soils but best on moist, deep, porous soils of northern exposure; will endure considerable drought . . .". Or again we should refer to the statements of Harlow and Harrar in their Textbook of Dendrology (1950): "Trees are found on a variety of soils but make their best

growth on deep, rich, well-drained porous loams in regions where there is an abundance of both soil and atmospheric moisture. . . . While [the Rocky Mountain form] most abundant on moist sites, it is quite drought-resistant and is often found on arid areas with ponderosa pine". It seems to be true that Schulman prefers dwarfed trees or those with "branching snag tops". In fact, the frontispiece of the publication (1945*b*) shows an isolated 15-foot Douglas-fir with a snag top and at least 60 per cent of the branches dead. These abnormal trees growing in the inhospitable environment of "upper steep and rocky slopes", where one would expect a minimum of soil moisture retention and a maximum of exported water, are said to give a record of the previous winter, October–June, rainfall. Therefore, "Logic suggests and experience has proved that the best drought-sensitive ring records come from upper, steep, and rocky slopes". With this emphasis on drought effects and lack of soil moisture at abnormal lower forest border sites, we must of course agree.

In southern California, "Only trees on dry, rocky slopes or ridges were selected for sampling; all sites were on the predominating granite" (Schulman, 1947). Adverse sites where growth is slow and highly variable are most fortunately located to yield trees for chronology (Schulman, 1951).

In the Big Bend National Park of Texas, cores were taken from a "sparse stand of Douglas-firs, stunted, slow-growing, and seldom reaching 20 inches in stem diameter", and "truly of an outlier character" (Schulman, 1951–52*a*). Nineteen cores, taken from Douglas-firs, represented almost all the mature trees of the area.

In the Ouachita National Forest of Arkansas, Schulman (1942*a*) took six cores from shortleaf pine which were "scattered over a well-drained secondary ridge top" at an elevation of 1300 feet. Three cores were from pines on a site with poor drainage which "would be considered an unsatisfactory source of specimens for climatic study in dry climates". These specimens showed sequences of growth layers that were "erratic and lacking in sensitivity". Turner (1936*b*, 1937), who also worked with the pines of the mountain areas of Arkansas, studied them in relation to soil and topography. On the steeper slopes, he said, stony areas and exposed rock were common. These situations obviously belonged to what Turner called inferior sites in contrast with in-

termediate and superior sites: " Sites with lower site indices are on soils with a high degree of slope and hence excessive water run-off, or extremely stony, or gravelly, or sandy soils with moderate or steep slope . . .". The poorest pine sites in Arkansas were on mountain soils where the slopes were excessive or where soils were gravelly or stony (Turner, 1937). Giddings (1941), who worked in central Alaska, sampled trees from sites which he described as " rocky faces of steep bluffs ", or again, " stocky, rather stunted, and malformed spruces rooted in thin, rocky soil high on a steep north slope ". However, he also took samples from trees which grew on lower slopes, river bottoms, and along river banks. It is of interest to note that he found different sequences of rings on different sites.

Smiley (1951) subscribed to the selection of trees apparently from abnormal sites, and it is of interest to botanists and ecologists to read that " Trees, in order to produce a climatic record, must grow under special conditions such as on a steep slope where ground water is present only after precipitation; they must have a definite growing season and react favorably to one controlling climatic factor ". What is the significance of the phrase, " react favorably to one controlling factor "? In the Southwest, Smiley said that members of the Pinaceae " give the best climatic records where they are found growing under severe conditions rather than under optimum ones. The forest border, where the forest thins out and stops (because of a climatic change) as the elevation decreases, normally has excellent climatic records present ". Thus, in summary, Smiley believes that trees give the best climatic records where located on steep slopes under severe conditions at the very edge of the lower forest border zone.

Weakley (1943), who worked in western Nebraska, selected his trees carefully and found that those " which grew on hillsides or on benches well above dry washes are most affected by moisture fluctuations and generally are usable ". On the one hand, trees " which grew wherever run-off or stored moisture increased the supply received by direct rainfall were not so responsive to yearly fluctuations of rainfall and consequently are of little or no value ". There is no word about runoff causing a decrease in the supply of water. On the other hand, " trees which have been in very exposed and difficult positions such as high south slopes or the tops of narrow sharp ridges generally have such compressed and distorted

rings that they too are of little or no value". These statements involve a nice sense of judgment of the correct amount of water to give a climatic record by inspection of the rings so produced. These clear statements by Weakley concerning the selection of trees in western Nebraska should also be contrasted with the somewhat more extreme statements concerning selection of trees under even more rigorous conditions in the Southwest.

Will (1946) worked on trees near Bismarck, North Dakota. His search was "confined to the sides of the many coulees leading down from the bluffs to the lowlands". Finally he found a burr oak growing on colluvial material whose slope upward from the oak was 35°. The construction of chronologies and their use as climatic records in western Nebraska and central North Dakota should perhaps take into account the work of Wiggin and Verduin (1946–47) who found that two annual rings were rather common for 1946 in southeastern South Dakota. In addition, multiple growth layers were far from rare on the High Plains of Texas (Glock, 1951).

Biologists and others have been guided apparently by their desire to study sites normal to a region and the effect of such sites on normal tree growth. Dale (1947), writing about drought in the Great Plains area, said that "it isn't the amount of water that falls which counts. The important thing is the amount of water that soaks into the ground and is kept there until crops can use it". With trees it would be the same, and the role of steep rocky slopes in view of what Dale said is obvious.

Many years ago Kapteyn (1914) held that trees should be taken from uniform conditions, with good subsoil water. He selected oaks from along the Main, Moselle and Rhine Rivers, and measured their rings. The results obtained appear to bear out the wisdom of his selections.

Recently Tarrant (1950) studied the relation of topography to site quality for Douglas-fir. The better sites are the concave lower slopes and depressions, whereas the poorer sites are the convex upper slopes, ridges and hilltops. In New England, Burns and Irwin (1942) measured amount of wood production as an indication of needle efficiency in white and red pine. They used trees in plantations on level land with porous homogeneous soil and no runoff.

In 1941, Friesner and Friesner compared rainfall to the growth

of trees from " sites subject, because of topography, to minimum amounts of run-off " (Friesner, 1950). In 1950 Friesner carried his work further in order to " determine the possible effect of a site where run-off, because of steep slopes, is certain to be high ". Agreement between tree growth and rainfall decreased notably on the steep slopes.

Giddings (1941), as before mentioned, did not confine his collections to trees growing on adverse sites but took them from river bank upward to timberline.

In north-central New Mexico Glock (1950) collected samples from trees which were growing in the upper part of the Transition Zone and lower part of the Canadian: ". . . the locations were chosen so that abnormal drainage toward or away from the trees was at a minimum ".

Gladwin (1940*b*) attempted to choose his trees " so as to give the widest range of environment within the area "; hence some trees were chosen from level ground and probably deep soil, others from steep slopes and probably shallow soil.

Hansen (1938) studied ring growth and the reproduction cycle in Engelmann spruce from near upper timberline in the Snowy Range of southeastern Wyoming. Although he took samples of trees on level surfaces or gentle slopes, the conditions were unfavorable because of thin quartzose soils, strong winds and low temperature. Hansen later (1941) studied ring growth in central Washington near the lower forest border. The collecting area lay on a sharp slope with shallow sandy soil. At places bedrock was exposed at the surface. Runoff is high during heavy rains and during the winter when the ground is frozen, which is important in view of the fact that less than 30 per cent of the mean annual precipitation falls during the growing months. The " physical factors of the environment are neither at an optimum nor in adjustment with one another ". Because of low summer rainfall and high temperature, growth is not normal, according to Hansen.

Hustich (1948*a*) worked near the northern limit of tree growth in Finland and his trees were situated " on dry moors in river valleys where drainage is sufficient ".

Lyon (1943, 1949), working in New England, selected trees from a variety of slopes and soil depths, and from upland and bogs. Even in humid New England, Lyon has emphasized, conifers

show "the dominance of the water supply factor in determining the relative width of the annual ring . . ." (1943). This contrasts rather startlingly with the insistence of workers in the Southwest that only trees growing under near-desert conditions with soil moisture in short supply yield a record of rainfall. Lyon said: "For hemlock and white pine, the correlations between relative growth rates and the precipitation records of certain periods of the year are so high that the occurrence of a notably narrow or wide ring of wood is presumptive evidence for a drouth or a generous supply of water to the tree for the growing season in which it was formed".

Paul and Smith (1950) pointed out that on steep slopes most of the precipitation runs away on the surface and therefore is not available to the roots of trees. Such a condition could stop growth during a season. In Indiana Reimer (1949) studied the growth of deciduous trees which grew on rather level land with fair to good drainage. Storie and Wieslander (1948) studied timber sites in relation to soils in California. The best sites were well drained, whereas the lower quality sites had either poor drainage or excessive runoff.

In summary, it is clear that recent studies emphasize three things: *a*) local site factors down to those at a single tree are of great importance in tree growth; *b*) local site factors are an interacting complex; and *c*) most students try to study normal trees growing under conditions normal to an area. The importance of local site factors, even around the single tree, was well emphasized by Gladwin (1940*b*). Among those who point out the complexity rather than the simplicity of site factors, attention may be directed to Briegleb (1945), Friesner (1943*b*), Gladwin (1940*b*), Huber (1948), Kienholz (1934–35), Moseley (1941), Shirley (1945), Tihomirov (1940) and Zeuner (1951*a*).

ANATOMICAL STUDIES

Little can be done intelligently with growth as a basis of interpretation until something is known concerning growth itself. Hence botanists have bent their prime efforts toward the ecology, physiology and anatomy of growth. Such growth applies to all parts of the plant body, to the entire stem and to the roots, to elongation and to diameter increase.

HEIGHT GROWTH OR ELONGATION. It would be impractical to summarize all work on this important topic. The material to which reference is made constitutes, it is hoped, a cross section of the chief trends of investigation having to do with the topic in hand.

The times of beginning and ending of elongation are spread over a considerable interval, depending, somewhat but not wholly, upon species and upon latitude or altitude for a particular longitude (Byram and Doolittle, 1950; Cook, 1940; Daubenmire, 1950–51; Friesner, 1942*a*, 1943*a*, *b*; Johnston, 1941; Kienholz, 1934–35, 1941; Pearson, 1950). In the case of growth initiation the time spread is less than that of growth cessation. Many species show the grand-period type of elongation behavior with the maximum rate-point spread over a time interval, whereas other species show a marked modification of the grand-period type of growth curve (Friesner, 1942*a*, 1943*b*). Some species begin growth early and stop early, others begin early and stop much later, and others begin late and stop early (Cook, 1940; Friesner, 1942*a*; Johnston, 1941; Kienholz, 1934–35, 1941). Friesner (1943*a*) learned interesting facts from a comparative study of elongation in primary, secondary and tertiary axes of two species of pine in Indiana. In general, the primary axes grew at a greater rate for a longer time than the secondary, and the secondary at a greater rate for a longer time than the tertiary. The outer or upper secondaries, however, elongated over a longer interval of time than those lower on the tree. For a period of more than two years the writer measured tip growth of trees in Maryland which grew within 20 feet of each other on a lawn. The time of growth initiation for all branches was spread over a very short interval. In contrast growth cessation varied all the way from early June to late September, not only among the trees but among branches of the same tree. It is clear, therefore, that the varying and variable time limits of the growing season for elongation provide a rather complex problem in the correlation of growth with one or more of the ecologic factors.

The time of extension and the time of radial growth do not by any means coincide. In India Chowdhury and Tandan (1950), working with broadleaved trees, found that the gap between extension and radial growth varied from two weeks to three months. This, they said, differs from Europe and North America where the

two activities begin at the same time. Such coincidence, however, is not exact. Kienholz (1934–35) found considerable variation among conifers in New England. With the orange tree Reed and MacDougal (1937–38) found that shoot growth preceded cambial activity by more than a month. Reimer (1949) worked with five species of deciduous trees in Indiana. All five exhibited the grand-period type of growth and belonged to the short-period type of axial extension. As regards axial elongation and radial enlargement, " It is rather well defined that these two types of growth are alternate ". This is shown by the following dates: *Prunus,* April 14–June 4 (axial), May 26–September 30 (radial); *Acer platanoides,* April 7–May 26, June 17–August 4; *A. saccharum,* April 14–May 26, June 10–August 25; *Tilia,* April 21–June 17, June 17–September 22; and *Fagus,* April 7–May 26, May 19–August 25. In general, Reimer says, axial growth is more likely to precede radial growth in deciduous trees than in conifers where the reverse may be true. Hustich (1945), working in North Europe, noted little quantitative correlation between length growth and radial growth of the same year; however, it was much higher with the previous year. Volume growth correlated very well with lengthening.

Many attempts have been made to correlate height growth with one or more of the meteorological factors which could conceivably influence growth at a particular time. Some attempts (Aaron, 1948; Craighead, 1941; Fowells and Kirk, 1945; Friesner, 1943*a*; Hustich, 1945; Kienholz, 1934–35; Pearson, 1950) have apparently yielded favorable results, others not so favorable (Cook, 1940, 1941*a*; Johnston, 1941), and still others a mixed reaction or a dependence upon other factors (Friesner, 1943*b*; Hustich, 1948*a*; Pruitt, 1947; Turner, 1936*b*). According to Cook (1940, 1941*a*), terminal growth has little relation to current temperature or rainfall in the Northeast; it is, instead, of a generic character. Fowells and Kirk (1945) found that height growth of ponderosa pine seedlings " was about proportional to the amount of soil moisture available and to the amount of water transpired ". In Indiana Friesner (1943*a*, *b*) found a mixed reaction: the type of growth curve in some species was little modified by external conditions, in others it was seemingly in agreement with temperature. The start of bud activity (1943*b*) depended upon environmental factors,

the most important being temperature; or (1943*a*) the start of elongation in pine depended upon growth substances released or elaborated by terminal buds. Hustich (1945) obtained rather high correlation between length growth and temperature of the previous year but only slight correlation between length growth and July temperature of the current year. A high temperature one year in North Europe gave long shoots the next year (1948*a*). Years of maximum flowering intensity in pine commonly coincided with years of long shoots (1948*a*). In New Hampshire, Kienholz (1934–35) studied leader elongation of pine. Growth did not correlate with daytime temperatures; however, it had a high correlation with minimum night temperatures and with mean night temperatures. Pearson (1950), working in northern Arizona, found that shoot growth during the early part of the season was a sensitive indication of temperature, whereas later soil moisture gained control. In fact, shoots attain greater length when April-May receive above average rainfall. Pruitt (1947), working in the Southeast, determined that a definite correlation existed between height growth and the relative position of the water table. From his observations in Arkansas, Turner (1936*b*) learned that rather high correlation existed between rate of height growth and soil series type. Much work remains to be done upon the factors which initiate elongation, guide it and stop it.

Uncertain as we may be concerning the strict conformity of elongation to climatic factors or the exact effect of growth-promoting substances, we may nevertheless reasonably expect to find evidence of growth fluctuations, even during the regular growing season, because of temperature and rainfall variations. Friesner (1942*a*, 1943*b*) noted elongation in Indiana both before and after what he called a mid-summer zero point. Such double waves of activity have been rather commonly noted; for instance, by Byram and Doolittle (1950) in shortleaf pine in the South, by Chowdhury and Tandan (1950) in broadleaved trees in India, by Friesner (1943*a*), by Kienholz among conifers (1934–35) in New Hampshire and among hardwoods (1941) in Connecticut, and by Reimer (1949) among hardwoods in Indiana. More than this, Friesner (1943*a*) detected " three waves of intensity " on the primary axis of *Pinus strobus* and *Pinus resinosa*. The writer measured tip growth for two years on a peach tree in Maryland and recorded a

mixture of two and three waves of activity per season. One branch with three tip increments in one season showed two distinct zones of terminal budscale scars within growth for that year. In addition, he has noted multiple tip flushes in West Virginia, Maryland, Texas, Arizona, and in the Sierra Nevada of California.

Waves of activity in terminal growth do not seem at all unusual during what is commonly called the growing season. More and more such fluctuations are being recognized by daily observation and measurement. There is some reason to believe that waves of activity occur nearly the year around, even during the winter or dormant season, though of course at a low level of intensity. This varies somewhat from the thought of Maximov (1930) who said that growth does not take place during dormancy, even though "external conditions may be quite favorable". So-called post-seasonal growth (Reimer 1949) could occur at any time after the mid-summer zero point of elongation or after the end of the grand period of growth, if such occurred, and before the rapid growth of the succeeding year. Spurts of post-seasonal growth following inactivity (after "plateaus" when periodic measurements of tip growth are plotted) and occurring within a growing season belong properly to that season; they may give multiple increments of tip growth. Here for the moment post-seasonal growth will refer to growth during late autumn and winter when dormancy occurs. Such elongation takes place either as true axial extension or as bud lengthening. Bell (1940) reported slow growth in length of the vegetative bud of the apple throughout the winter months in Nova Scotia. Activity in the bud, including differentiation and actual lengthening, have been noted by Friesner (1942*a*), Hustich (1948*a*) in Finland, Kienholz (1941) in Connecticut, and Reimer (1949) in Indiana. However, a slight amount of true axial elongation does occur (Friesner 1942*a*; Kienholz, 1941; Reimer, 1949). Evidence of bud elongation as well as of true axial lengthening has been gathered by the writer in Texas.

DIAMETER GROWTH. From an ecologic standpoint, growth layers give a more satisfactory record than do increments of elongation because growth layers are more sharply delimited and because they are more permanent. Several studies of the past decade bear directly upon the gross anatomy of growth layers, although no doubt much work remains to be done.

Inspection of a growth layer over its entire areal extent in a stem requires complete dissection of the tree. However, the differences found in different parts of the trunk as well as the unknown occurrence of partial growth layers makes dissection a requisite to complete knowledge of growth-layer distribution. Brown (1912) noted that the width of a complete ring decreased from apex to base in *Pinus rigida* from New York state. In New England, Burns and Irwin (1942) sectioned more than a score of red and white pines and found that the increment for 1940 had its maximum thickness at heights of 17 to 19½ feet in trees 20 to 24 feet high. They did not use increment borings because " the width of an annual ring at any level is not directly proportional to the annual increment's total volume ". Growth-layer thicknesses are taken on a linear basis, whereas total growth occurs on a volume basis. In contrast to the foregoing, Paul and Smith (1950) studied 75 southern yellow pines and found that wider growth rings were more prevalent in the lower than in the upper part of a tree.

In the Southwest, Krauch (1949*a*) examined the growth of Douglas-fir in relation to age. Best diameter growth occurred during the mature stage after the tree reached 240 years. Later, diameter growth decreased, although growth in the basal area continued at a high rate with a maximum occurring at age 340. Marr (1948), in his enlightening work near the forest limit east of Hudson Bay, found excellent circuit and longitudinal uniformity in relative thicknesses which asymmetry of trunk did not alter. An extreme case of asymmetry caused by the wind has been cited by Oosting (1948) in connection with a Monterey cypress from California collected by W. S. Cooper. The windward side contained 50 growth rings, whereas the leeward had 304.

Church (1949) has brought together a mass of information from the literature on the effects of defoliation by various agents on the growth of certain conifers. Because of the importance to growth-ring studies, the summary by Church cannot be passed over. Defoliation of spruce and balsam fir by the spruce budworm caused different degrees of retardation of growth in different parts of the crown: severe reduction in the top of tree, no change in the middle, and a decided increase near the base. When the budworms stopped feeding, a second depression of growth might occur because of heavy production of cones. Severe feeding could cause total sup-

pression of rings on parts of the trunk, although the spruce that recovered " showed no indication of missing growth rings ". The first result of defoliation of tamarack by the larch saw fly appeared as an absence of thickened tracheids in the autumn wood. Subsequently there was a reduction in the thickness of growth layers and in some cases an absence of growth in the base of the tree. A growth layer, however, was formed in the crown during every year until death. Defoliation by fire resembled that by insects in as much as reduction of growth took place for the most part in the lower portion of the tree. Defoliation by hail storm also retarded growth. Such a storm defoliated a young longleaf pine at the end of April, 1937, after most of the spring wood had been formed. As a result, only a narrow band of summer wood was formed, a circumstance of note when it is recalled that thin summer wood has also been ascribed to drought. The spring wood of 1938 was much less than normal and the summer wood exceeded it in thickness. In 1939 growth was still much below normal. Artificial defoliation indicated that gradual reduction in increment occurred after partial defoliation or after early spring defoliation of new growth among certain conifers. Late spring defoliation of new growth in jack pine gave greater reduction of wood in the top of the tree and killed it the second season. In contrast, early removal of old foliage gave decided reduction of ring thickness at the base of trees in years of defoliation. In summary, Church said that the degree of defoliation determined the amount of reduction in growth, that the reduction in diameter growth did not take place at uniform rate throughout the stem, and that in most cases the greatest reduction took place in the basal part of the tree.

Thus it appears that under both normal and abnormal conditions diameter increases vary within the stem of a tree. Such variations must be considered where growth-layer thicknesses are used as a straightforward measure of some one ecologic factor.

Studies made on portions of a growth layer, either the light- or densewood, have given somewhat diverse results. Church (1949) reported the formation of a narrow band of summerwood because of defoliation; Marts (1949, 1950) and Paul (1946) used pruning to decrease the springwood and thereby increase the percentage of summerwood; Paul (1944, 1946) and Paul and Smith (1950)

noted that a lack of summerwood was due to a deficiency of soil moisture during the growing season; and Schulman (1942*a*) correlated summer rainfall with summerwood formation. In the South, Paul and Smith (1950) and Schulman (1942*a*) found little variation in thickness of springwood; variations in summerwood responded to summer rainfall. Douglass (1946*a*) did not mention the possible cause of thin or weak late woods. To him a thin latewood following a wide earlywood signified a double or intra-annual ring.

It is clear that experimental work on the gross constituents of growth layers, such as was done by Marts, and Paul and Smith, are highly desirable in addition to the painstaking statistical work of Schulman and others. The matter, however, may be carried further, into detailed anatomical studies.

In eucalyptus, Amos, Bisset and Dadswell (1950) found the shortest fibers in earlywood and the longest in latewood, the change occurring suddenly. They established "an intrinsic relationship between growth rate and fibre dimensions". Bisset, Dadswell and Amos (1950) extended the foregoing results by pointing out that variations in fiber length followed a characteristic pattern throughout the growth rings of trees in temperate climates. In New Guinea, where definite growth rings were absent, "there was no significant fibre-length variations in the wood laid down over several years". In fact, "there must be a close relationship between cell dimensions and growing conditions". Johnson (1942) worked with three species of *Populus* in Canada and found that fibers in fast-growing annual rings were longer on the average than those in slow-growing rings from the same tree. In single rings, fibers of earlywood were shorter and thicker than those of latewood. This evidence appears to be conflicting if earlywood grows faster than latewood. Wardrop (1951) related tracheid length to growing conditions, age and rate of division of cambial initials, and applied the information to growth of trees for lumber. If certain trees of the same species in the same group possessed longer tracheids in the first growth layer, then subsequent growth layers also had long tracheids. Thus nursery stock for strong lumber could be selected. Church (1949) noted that the first result of defoliation was the absence of thickened tracheids in autumn wood. Total vessel length in ring-porous and diffuse-porous hard-

woods was studied by Greenidge (1952). In the more highly specialized ring-porous woods vessels might extend the full length of the stem, whereas cross walls restricted the length of vessels in diffuse-porous woods. Therefore the " vertical rates of water conduction in large woody stems may be closely correlated with total vessel length ". A study of gymnospermous woods as well as the hardwoods suggested to Greenidge " that due regard should be given to the patterns of moisture retention in addition to moisture movement in any study of the water economy of a species ", a suggestion of value for the understanding of the fundamental relation between growth and climate.

One more point should be mentioned—the work of Amos, Bisset and Dadswell (1950) on eucalyptus. Early in the 1944–1945 growing season the water balance was overtaxed, as shown by a saturation deficit and temperature higher than normal and a rainfall lower than normal. This produced a type of anomalous tissue near the start of the growth layer which resembled somewhat the frost injuries described by Glock (1951). In the one case the injury was due to drought, in the other to frost.

MULTIPLE GROWTH LAYERS. The problem of multiple growth layers in a single year is a difficult one, and its proper solution bears directly upon the validity of much tree-ring work. Such difficulty is highly important because so much of current work uses trees grown under the variable ecologic conditions of forest zones adjacent to the arid regions. It is self-evident that a study of cambial activity is fundamental to an understanding of its periodicity, whether intra- or inter-seasonal.

Among those who have detected a single period of cambial activity are Byram and Doolittle (1950) in the shortleaf pine of the South, Friesner (1941) in the beech of Indiana, Friesner and Walden (1946) in *Pinus strobus* of Maine, and Chowdhury (1940) in three species of diffuse-porous wood in India. Friesner and Walden contrasted their results with those of Brown (1915) who found two periodic optima of growth in *Pinus strobus* of central New York, one during May and early June, and the other in July and August. Other students, concentrating on the growth layers themselves, have observed doubles absent or rare: Hustich (1948*b*, 1949), among conifers at the polar border in Finland; Marr (1948), among conifers at the polar border on the east coast

of Hudson Bay; Moseley (1941), among hardwoods of the Northern States; and Will (1946), in an oak near Bismarck, North Dakota.

In the detailed work of Hustich (1949) and Marr (1948) close observation and careful statement provide convincing argument for the unity of the annual increments. In contrast, Moseley (1941) stated: "In the Northern States I have never found a hardwood tree of any kind . . . that formed two rings in one year". The statement might be regarded as rather broad. In North Dakota, Will (1946) did not expect trouble from double rings because "the season is generally too short to allow the double ring formation".

Questions raised and observations made by Brown in 1912 carried highly suggestive ideas for students of tree growth. Double rings, he found, were common in New York and "might easily cause miscalculation as to age". In broadleaved trees doubles were ascribed sometimes to defoliation and at other times to favorable and unfavorable external factors. In *Pinus rigida* double rings must have been caused by external factors.

Among those who have detected multiple periods of cambial activity within a season are Chowdhury (1940), in one species of ring-porous wood from India; Daubenmire and Deters (1947–48), among deciduous and evergreen trees in the summer-dry climate of Idaho; Friesner (1942*b*), in two species of broadleaf trees in Indiana; Kienholz (1934–35), in red pine of New Hampshire; and Reimer (1949), in four out of five deciduous species in Indiana.

Double rings whose presence has been determined by the growth layers themselves have been noted by Dobbs (1942) in England; by Glock (1951) among many species in West Texas; by Senter (1938) especially among oaks of the Middle West; by Weakley (1943) among red cedar and ponderosa pine of western Nebraska; by Wiggin and Verduin (1946–47) among nine species of hardwoods in South Dakota; by Schulman (1940*c*) along the California coast, the Pacific Northwest (1945*a*), in Southern California (1947), in South Texas (1951–52*a*), and in Arkansas (1942*a*); and by Douglass (1946*a*), Gladwin (1940*b*), Hawley (1939, 1941) and Schulman (1941, 1945*b*, 1951) in the Southwest. If one interprets their explanations correctly, he concludes that Douglass, Gladwin, Hawley, Schulman and Weakley feel rather confident of

their ability to detect false rings by their fuzzy outer borders, by their positions within the annual increment or by crossdating. The relation of double rings to crossdating will be discussed later.

Several of the above studies call for special remarks.

In Idaho Daubenmire and Deters (1947–48) observed growth slow-down in mid-season due to low temperature. As a matter of fact, growth rate as measured by dendrometers varied from slowing down to actual shrinkage. This basic work of Daubenmire and Deters is highly suggestive as regards an ultimate understanding of cambial activity and the course of growth. Reimer (1949), using dendrometers on deciduous trees in Indiana, observed two peaks of growth in *Prunus,* two peaks in two species of *Acer,* and three peaks in two species of *Fagus.*

Douglass (1946*a*) and Schulman (1951–52*a*) suggested that proper illumination and a surface cut diagonal to the grain give the best means of distinguishing annual from non-annual rings. In addition, Douglass said that a double ring in the Southwest commonly has the following sequence: wide earlywood, faint latewood, narrow earlywood, and heavy latewood. This was true especially if the faint latewood was hazy. However, Church (1949) recorded the same sequence as comprising two annual rings, the faint summer wood having been caused by a storm which defoliated the tree. If the faint band of latewood occurred close outside (toward the bark) the heavy band of latewood, according to Douglass, the sequence comprised two annual rings. The writer, however, has observed hundreds of cases of faint densewood bands just outside heavy bands in West Texas, and all of the heavy bands were part of an intra-annual (Glock, 1951).

Douglass (1946*a*), Gladwin (1940*b*), Hawley (1941) and Schulman (1941, 1945*b,* 1951) in the last analysis have claimed a solution of the difficulties inherent in double rings by means of crossdating. In this connection Schulman (1945*b*) has aptly remarked that " at the lower forest border . . . false rings tend to appear at times indistinguishable from true annuals ". He found the same to be true in California (1940*c*). As a summary he wrote (1941): " There exists a complete array of types of false annual rings ranging from those which are extremely ill-defined to those which cannot be differentiated from true annual rings until they are cross-dated ". And a step farther was taken by Douglass

(1946*a*): " Crossdating . . . put exactness into the dating of tree rings . . . the feeling of precision in our chronology building has grown stronger and stronger . . . . We were fortunate . . . in having a large climatically homogeneous area . . .". In view of the above quotations it is highly pertinent to refer to the work of Dobbs (1942) who studied over 100 sections of larch that came from an area of 50 mile radius around Bristol, England. Double rings were so common that Dobbs used them for crossdating purposes: " there was a general and recognizable pattern formed by the false rings ". Therefore, if intra-annuals exist which are indistinguishable from true annuals, and which occur in areas climatically homogeneous, it is difficult to see how crossdating alone can reveal their intra-annual character.

A final point in connection with double rings must be mentioned. Weakley (1943) in western Nebraska and Wiggin and Verduin (1946–47) in southeastern South Dakota had difficulties with double rings, and Weakley even with triples, whereas Will (1946) had no such difficulty in south-central North Dakota. He said: " In this northern region that difficulty seems to be very slight as the season is generally too short to allow the double ring formation ". It has been recorded, of course, that Friesner and Walden (1946) found only one peak of growth per season, that Marr (1948) gave strong evidence for unity of the annual increment in trees on the east coast of Hudson Bay, and that Moseley (1941) had never found a double in the northern States. In addition, it has been recorded that Brown (1912, 1915) detected double rings prevalent in central New York, that Kienholz (1934–35) found two peaks of growth in New Hampshire, and that Friesner (1942*b*) traced two peaks of growth in Indiana. Somewhere between the polar border of the forest, as recorded by Marr and by Hustich (1949), and South Dakota, New York and New Hampshire the single annual increment of the north gives way to the double tendency of the south; it would be most interesting indeed if the transition occurred between North and South Dakota. However, we shall await more evidence. Schulman has said (1945*b*): " It has been observed by Douglass that in the Southwest ring duplicity (*sic*) in this species (*Ponderosa pine*) was of increasingly frequent occurrence with decreasing latitude ". Is the problem so simple?

ROOT GROWTH. In Pennsylvania, Wood (1934) studied roots because, as he said, " so little is known of the root systems of forest trees larger than seedlings and because most of the major problems of silvicultural practice in the forests of the eastern United States are linked in some way with roots ". The roots of a chestnut oak comprised 45 per cent and the trunk and branches 51 per cent of the total weight of the tree; the crown spread covered 22 square feet, and the root spread, 229 feet. Undoubtedly the root system makes up an important part of a tree. In her study of grass roots in Rhode Island, Stuckey (1941) wrote that: " Root growth and its influence on the subsequent development of the plant has always been recognized as important in respect to food and water relationships . . .".

The growth of roots occurred in two spurts during a growing season, as shown by the work of Harris (1926) with apple and filbert roots, of Kaufman (1945) with jack pine in Minnesota, of Kienholz (1934–35) with certain conifers in New Hampshire, of Pessin (1939) with longleaf pine and associated species in southern Louisiana and Mississippi, of Preston (1942) with lodgepole pine, of Stuckey (1941) with grasses in Rhode Island, and of Turner (1936*a*) with two species of pine. Harris and Turner ascribed the mid-season resting period to lack of soil moisture. In Minnesota, Kaufman ascribed reduction of rate of root growth to a drop of available moisture to less than four per cent and a high rate of evaporation. Morrow (1950) observed the growth of roots of sugar maple throughout a mild winter in central New York. Early autumn drought stopped root growth. He asserted that: " Shoot growth, cambial activity, leaf activity, and root growth demonstrated no correlation, except that the maximum growth of each occurred during the same period of the year ". Stuckey noted that cell division in root tips occurred at temperatures very close to 32° F. and took place slowly all winter.

To some it may be new to learn that root systems are in the main surprisingly shallow. This has been shown by Le Barron (1945) with black spruce in Minnesota, by MacAloney (1944) with jack pine, by Pessin (1939) with longleaf pine and associated species in southern Louisiana and southern Mississippi, by Preston (1942) with lodgepole pine, and by Scully (1941–42) with hardwoods in Wisconsin. Bannan (1941–42) found that the lateral roots of

Thuja were no deeper than six inches and most of them only two or three inches deep. Le Barron observed that spruce in northern Minnesota had a shallow spreading root system, no matter whether the soil was well or poorly drained. In southern Louisiana and Mississippi, Pessin found most lateral roots in the upper one foot of soil. Under normal rainfall pine seedlings and associated plants obtained plenty of soil moisture, but during drought the trees suffered because grasses took so much of it. Preston found the majority of roots of trees one to 15 years old in the upper six inches of soil, and a tendency to increase the average depth with age. The lateral roots of greatest length were almost invariably shallow. Roughly speaking, Scully found that the upper eight inches of soil contained 80 per cent or more of the total root volume.

Bannan (1941), working with the variability of wood structure among the roots of eight species of conifers native to Ontario, chose his materials from different habitats and from different parts of the root systems. The proportions of early- and latewood, the size of tracheids and the thickness of their walls varied greatly in different parts of the root system and in different specimens. No consistent relationship existed between soil moisture and tracheid size; there was much dissimilarity between trees of the same species growing under like soil conditions, and sometimes the same diverse tendencies between roots of the same tree. More such work on anatomy, or ecologic anatomy as it were, is highly desirable.

The writer does not presume to be able to select all important contributions on the anatomy of tree growth. He does hope to give some idea of the range of current studies and, perhaps, of the need for prolonged programs of basic research on the course of growth throughout the year, the variations in that growth and its causes. Many workers have contributed to a growing body of knowledge, the following work being selected as typical: Anderson (1951) on tracheid length in conifers; Bannan (1941–42) on wood structure of *Thuja,* tracheid size and distribution of parenchyma cells; Barghoorn (1941) on the absence of rays because of specialization or unfavorable environments; Barrett and Downs (1943) concerning the effect of pruning on diameter and height growth; Bethel (1941) on the relation of maximum fiber length to height of tree among six dissected loblolly pines; Bruce (1951) on the

relation of height growth to fire and soil quality; Cook (1941*a*, *b*) on the period of height growth in ten conifers and six hardwoods in New York in which he found that the shape of the growth curves is constant, appears to be characteristic for each species and is not affected materially by temperature or rainfall unless it be drought; Downs (1943) on release of white pine in the southern Appalachians from a hardwood overstory; Gindel (1944) on false rings in Aleppo pine of Palestine as a result of interspersed periods of favorable and unfavorable growing conditions outside of the regular dormant season; Jacobs (1939) on the reduction of diameter growth near the base of a tree by prevention of sway; Ladefoged (1946) on the increase of diameter growth with an increase in crown size in the spruce of Norway; Lommetzsch (1940) on tracheid length and differences of lignin content between Germany and western Norway; Meagher (1943) on height growth of piñon and juniper seedlings little influenced by shade or watering; and Wilde and Voigt (1948) on wood density in jack pine in relation to soil fertility and drought resistance, frost injury and parasite attacks.

PHYSIOLOGICAL STUDIES

BASIC NATURE. Some time ago Illick (1915) stated that "Growth rings have a physiological origin". That is true today. Any work which neglects the physiological aspects is, we think, merely a preliminary approximation. However, here we should feel presumptuous to infer an ability to review critically all pertinent literature. Work has come to our attention and, where possible, we have applied it to our problems. For the application of the great body of physiological knowledge to growth layers we depend upon the plant physiologist and the biochemist.

Kramer (1943) stated that: "Variations in the environment can produce variations in tree behavior or growth only in so far as they affect internal physiological processes and conditions of the tree". The behavior of trees depends upon the interaction of hereditary and environmental factors. In 1948 Kramer wrote on plant physiology in forest research. The hereditary potentialities of trees operating in an environment by means of internal physiological processes and conditions produce tree growth. Much work remains to be done. Of this Thornthwaite (1940) was well aware. He wrote: "The problem of atmospheric moisture in relation to

ecologic problems is still far from being solved. When ecologists acquire a basic understanding of the process of moisture transfer between the land surface with its vegetation and the atmosphere, the inadequacy of present measurements of atmospheric moisture and the futility of attempting to determine relationships between simple functions of atmospheric moisture and physiological functions of plants will become apparent".

One is loathe to give examples which illustrate a possible lack of basic knowledge of plant physiology and anatomy. Only two will be given, without comment. "The question of records of swamp trees is puzzling until one remembers that for growth the roots of a tree must take in food as well as water. Food is obtained ordinarily through breakdown of the mineral material surrounding those roots. For this, oxygen as well as water is necessary. If the interstices between particles of soil are so filled with water that almost no oxygen is present, the tree is stinted in food and hence will not produce as large a ring as though the soil were dryer" (Hawley, 1941). Or again we may read: "Just under the bark is the growing layer which produces one true ring per year. This ring consists of fairly soft wood made up of large cells which grow quickly in the spring and of smaller cells with dark, thicker walls which grow in the summer and whose extra thickness protects the tree in cold winter weather while it is not growing" (Senter, 1938).

The work of Veihmeyer (1927) symbolized the serious work involved in understanding physiological factors. In studying these factors students have ranged widely, from scepticism on the influence of the moon (Beeson, 1946) to emphasis on the importance of growth-promoting substances. Apparatus has been devised (Studhalter and Glock, 1941, 1942) and programs organized (Glock and Studhalter, 1941) for the purpose of tracing the course of growth throughout the year. Food reserves and nutrient ratios have been emphasized by Asana (1950), Blackman and Wilson (1951), Friesner (1943*b*), Gibbs (1940), Handley (1939), Hull (1952), Humphries (1950), Judkins (1949), McComb and Kapel (1940), Mitchell and Chandler (1939) and Turner (1943), although none has excluded the influence of other factors. For instance, Handley found that chilling to near freezing brought radial growth almost to a standstill, impeded the movement of

starch from leaves, and cut down water conduction to the wilting point. Available water either as soil moisture or rainfall, or other external factors, has been studied by Friesner (1943*b*), Friesner and Friesner (1941), Kramer (1941, 1944, 1945, 1950), Scofield (1945) and Thornthwaite (1945*b*). With respect to rainfall, Friesner said that " it is apparent that tree growth reflects rainfall only when the latter is such as to influence the physiological processes of the tree ". Kramer gathered together much information on soil moisture. As soil moisture declines, the effects of such decline are exaggerated; he stated (1941) that: " The results . . . indicate that water probably is not equally available to plants over the range from moisture equivalent to wilting percentage, but becomes less available with decreasing soil moisture ". This may have importance because " almost everywhere soil moisture is sometimes deficient " (Thornthwaite, 1945*b*). Internal factors were stressed particularly by Friesner and Walden (1946) and by Kienholz (1934–35). Stone, Went and Young (1950), becoming interested in Coulter pine of southern California, which can survive long periods of drought on shallow soils, found that aerial parts took up water from the atmosphere—negative transpiration.

GROWTH-PROMOTING SUBSTANCES. Growth-promoting and inhibiting substances are occasionally referred to by some investigators as though they give us a final answer to our questions about growth. This is not quite true. We still want to know how the substances act and what factors control them. From the complexities involved in the production and application of growth-promoting substances to the apparent simplicity of comparing tree growth and rainfall there is seemingly a large gap. However, we would be grossly unfair if we assumed that a student is unaware of the action of auxins and enzymes simply because he does not treat them at length in each of his writings. Much detailed work has appeared on growth-promoting substances, and the pages of this magazine have carried valuable reviews. Mention will be made here chiefly of those works which refer to growth-promoting substances as an adjunct to their prime interest. Among these are Aaron (1948) who spoke of the effect of enzymes on cambial activity and solution of stored foods; Ashby (1950) who studied the action of hormones or the level of some nutrient on the meri-

stems; Avery, Burkholder and Creighton (1937) who considered a hormone as a cambial stimulus; Baird and Lane (1947) who found a double peak in summer in seven out of ten species of wild plants; Brain (1940) who found that external factors could influence auxin direction into a transverse stream and thereby influence secondary growth; Chowdhury and Tandan (1950) who distinguished between two types of auxins, one to give extension and the other to give radial growth; Evenari (1949) who wrote on germination inhibitors; Fraser (1949) who studied the effects of heteroauxin on the development of the components of an annual ring; Friesner (1942*b*) who said that growth rhythms "are most likely due to internal physiological conditions, such as available hormones", and (1943*b*) who thought that enzymes and growth hormones were responsible for modifications of the symmetrical grand-period curve of growth; Hackett and Thimann (1952) who studied increase and decrease of water uptake as influenced by auxins; Messeri (1948) who studied the relation between cambium divisions and growth-promoting substances; Reed and MacDougal (1937–38) who thought auxin induced cambium growth; and Wareing (1950) who studied the dependence of extension and radial growth upon auxins. Using a branch of *Pinus strobus,* Fraser (1949) prevented formation of densewood by application of β-indole acetic acid (heteroauxin).

Studies concerning growth-promoting substances may be of first importance to those who work with tree growth. Scientists, it seems, will be hesitant to accept the opinion of Abbott (1946) who said: "It is of little consequence that no one knows just how a tree is able to grow". He was speaking of tree-ring work.

FRUITING AND SEED YEARS. Perhaps in our work on tree growth we have neglected the effects of fruiting and seed years. Even Antevs in 1925 wrote: "Abundant production of seeds causes a reduction of the radial growth during the seed year. The decrease in growth may extend to the following year and then be greater than during the seed year itself". Two years later Büsgen-Münch called attention to the effects of the formation and ripening of fruit on radial growth of pine. Tovstoles (1938), said Hustich (1945), pointed out that minima in the curve of radial growth of pine in Ukraina depend on the seed year. Others who have been conscious of the effects of seed year or fruiting on

growth are Hall (1949), Hodson and Zehngraff (1946), Hustich (1941, 1948*a*, 1949), Pearsall on papers by Singh (1950), and Scarth et al. (1947). If a " seed year " is responsible for a thin growth layer, how can we distinguish it from one which is thin from alleged drought? Hustich (1949) referred to Renvall who said that the intervals between seed years near or at timber line were long and irregular, occurring more frequently in recent decades, at least three in 20 years.

CROWN SIZE. In general, crown size or total leaf area affects, through food manufacture, the amount of xylem laid down (Badoux, 1946; Burns and Irwin, 1942; Gevorkiantz 1947; Mowat, 1947). The same does not apply so well in the Southwest (Pearson, 1943, 1950; Wadsworth, 1942). Wadsworth stated that " the rate of growth of ponderosa pine is much more closely related to environment than to crown size or age ". Pearson (1950) stated the matter even more definitely: ". . . a relatively small leaf surface is sufficient to handle all the photosynthetic activity that the limited water supply can support . . .". Such information can assist to an understanding of the effects on xylem formation of natural pruning through storms.

GROWTH RATE. The subject of growth rates involves so many complexities that the writer hesitates to refer to it. A single point only will be mentioned, the distance over which uniformity prevails. Miss Hawley (1941) obtained log ends from sawmills in the Mid-West. As to location of the original trees, the mill men knew " at least the approximate area being cut over at the time, a section usually within a fifty mile radius of the mill ". One is then a bit startled to read: " The tree-ring areas have been found to be so large that this approximation of location is close enough for all the work except that of special botanical and ecological interest . . .". Lyon (1943) worked with evergreens in New England: " The agreement between sites is highest when the trees are of the same species and the sites are not many miles apart. A distance of 50 miles apart is not too great for this type of cross-identification under conditions involving no other factors such as coastal effects or differences in elevations ". In contrast with the above, MacDougal (1923) noted that " two trees within 20 meters of each other at the Coastal Laboratory, at Carmel, California, are so differently placed that one made a basal layer of

wood 8 mm. in thickness during the last season, and the other one a layer 0.75 mm. in thickness". Thus the influence of local topography and drainage. Glock (1950), working with conifers in New Mexico, found moderate disagreement between species and between members of the same species: "Partial disagreement among the various trees, growth layer to growth layer, emphasizes a definite localization of site factors to each tree. Disagreement among the trees increased with increasing distance, distance measured in yards rather than in miles".

INITIATION AND CESSATION OF GROWTH. Variation in the time of growth initiation and cessation is bound up so intimately with the factors, external and internal, causing or inhibiting such growth, that some attention must be given to the subject. In 1944 Burns warned of the "futility of using averages to describe physiological conditions in a plant habitat". For instance, if one compares tree growth with a growth factor which includes the same time interval year after year while the growth period varies, one could hope merely for results approximating those derived from a knowledge of the precise time of impact each year.

The spread of opening and closing dates for growth has been reported by different workers, among whom are Bonck and Penfound (1944), Chowdhury and Tandan (1950), Cook (1941*b*), Daubenmire (1945–46), Daubenmire and Deters (1947–48), Fowells (1941), Friesner (1941, 1942*c*) and Giddings (1941). In India, Chowdhury (1940) observed that growth in trees of the same species began over a range of one to three weeks. Cook (1941*a*) worked with trees in eastern New York during 1940. For 16 species growth initiation was spread from May 7 to June 9; cessation ranged from June 20 to September 16. The period of growth varied from 35 to 101 days. Daubenmire (1950–51), using different races of ponderosa pine at a station, found a spread of at least five weeks in growth initiation and almost four months in cessation. Friesner (1942*b*) noted a growing season of nine weeks for *Fagus* in 1940 and only five weeks in 1941. Friesner and Walden (1946) studied two specimens of *Pinus strobus* for five years, 1941–45. In sequence for the years given, one tree began radial enlargement April 26, May 2, May 22, April 15 and May 26; the other tree began May 3, May 2, May 15, April 29 and May 5. Growth ceased on the first tree the week ending

Nov. 1, Oct. 31, Oct. 16, Oct. 7 and Oct. 6; on the second tree for the same years Nov. 1, Sept. 19, Sept. 18, Oct. 7 and Oct. 6. Kienholz (1941) divided his trees into short season and long season, the former completing 90 per cent of their growth in 30 days, the latter 90 per cent in 60 days. MacDougal (1936) noted among six species of trees a period of radial growth varying from 50 or 60 days to 133 days. Reimer (1949) measured radial enlargement on five species and found the interval during which it occurred to vary from eight to 19 weeks. Schulman (1945*b*) collected increment cores in the Colorado River basin, and with them as a basis he noted that the start of cell growth varied from mid-May to early June.

Perhaps the variations mentioned above help clarify some of the difficulties encountered in a rigid time comparison between growth and the factors favoring it.

GROWTH RHYTHMS. The length of the growing season varies all the way from 12 months in the tropics (Shirley, 1945) to two months or so above 56° north latitude (Marr, 1948). "Annual rings are found only in regions with climatic periodicity, an alternation between cold and warm, or rainy and dry periods . . ." (Hustich, 1948*a*). The alternation may cover a year or a portion of a year. Fluctuations in growth factors are not necessarily on an annual basis; moreover, temperature and rainfall are not the sole factors having to do with tree growth. In so far as rainfall is concerned it can be evenly spread over the year, it can come in winter or in summer, it can be divided into two rainy seasons per year, it can fall in quantities sufficient to maintain soil moisture at a high level, or it can fall so infrequently that soil moisture may drop below the wilting coefficient between showers. This is but one factor. Perhaps growth does not wholly cease throughout the entire body of a tree during any part of a year (Bell, 1940). Fluctuations in any one of the host of growth factors or changes in their interrelationships may well cause variations in cambial activity and in rate of growth, amount of growth and times of growth. If growth factors are actually growth factors, then growth will result whenever they operate effectively; and that may be once a year, or several times, depending upon the time of impact and the speed of physiological and anatomical responses. Variations in process or structure have been noted, for instance, by

Baird and Lane (1947), by Friesner (1941, 1942*a*, *b*), by Hawley (1939, 1941), by Hummel (1946), by Kienholz (1934–35, 1941) and by Schulman (1945*b*, 1951–52*a*).

This matter of cambial rhythm has great importance in studies on the course of growth. A body of evidence has accumulated to show that the rhythm varies in amplitude from a degree so mild that the results are barely perceptible to a degree so intense that the results are sharply bounded increments of growth. In addition, the evidence indicates a rhythm whose wave length may vary from a year or more down to a matter of several days or less.

Southern pine has been reported (Byram and Doolittle, 1950) " to put forth two or more leaders during a growing season, which may last from five to eight months, depending on the latitude ". Except for minor disturbances radial growth did not show periodic spurts. Darrow (1943) made interesting observations on the ocotillo (*Fouquieria splendens*) which grew under two rainy seasons per year. At first terminal growth is fast and occurs yearly; on the approach of maturity it becomes more and more sporadic and ceases when the branches are ten to 15 feet in length: " During the years characterized by widely-separated storm periods within a rainy season, ocotillo plants may have several periods of foliation and defoliation ". Ordinarily the ocotillo leafs out twice a year, at the start of the winter-spring season and at the start of the summer season.

Daubenmire (1945–46), in studying trees at different altitudes in Idaho, found that ponderosa pine ceased growth in early July at his lower station because of abnormal heat and dryness. After a week of moderate temperature and showers the normal rate of growth was resumed. *Thuja plicata* at the lower station had two distinct growing seasons interrupted by a period of quiescence in late August. The second growing season began with the first showers of the rainy season. Daubenmire and Deters (1947–48) measured trees on the campus of the University of Idaho. Both deciduous dicots and evergreen conifers grew for a few days early in April, 1944, in response to a brief period of above-average temperature. Then the trees were inactive during two weeks of cool weather. A smoothed growth curve of *Pinus* would show no absolutely quiescent period all year around.

Fielding and Millett (1941) worked on diameter growth of

Monterey pine in Australia. At Canberra, with its dry tableland climate and irregular rains, the only clearly defined period of diameter growth was in the spring; in summer and autumn bursts of growth followed soaking rains. At Mount Burr with its more favorable forest climate and seasonal rains, there were two main periods of diameter growth, one in the spring and the other in the autumn. Important bursts of growth were associated with any soaking rains during the drought of summer.

Handley (1939) chilled tree trunks down to a temperature a few degrees above freezing for the season of growth and found that he had prevented thickening and lignification of the outer rows of cells. Tharp (1939) studied purple sage in trans-Pecos, Texas. The shrub " bursts into a profusion of rose-colored bloom any, and every time, from spring to fall, that sufficient rain comes to it ".

In southern California Reed and MacDougal (1937–38) noted a characteristic periodicity in the growth of shoots on citrus. A graph of cambial increments showed three peaks of growth. In West Texas, Glock (1951) observed the course of growth and found periods of cambial activity within a season which gave multiple growth layers. Reed (1928) studied lemon trees in southern California and, measuring growth from May 1 to October 23, found that 94 shoots had three distinct cycles of growth, whereas 17 had only one cycle. The one-cycle shoots paralleled the other shoots for the first four weeks of the season and then were completely arrested: " Annual fluctuations in the growth rate of plants are well known, but intra-seasonal cycles are less prominent ". As a final note on growth rhythms the work of MacDougal (1923) may be cited. In July, 1919, formation of wood in Monterey pine ceased at Carmel, California, when water in the soil dropped to five per cent. One tree was irrigated for two days. It resumed growth and put down xylem of greater thickness than that earlier in the season.

CAMBIAL INACTIVITY AND DEATH. Growth rhythms composed of alternating periods of high and low activity, or of activity and no activity, lead directly into the problems of cambial dormancy with respect to cell division and what tree-ring students call " missing rings ". By " missing " they no doubt mean absent on the cores or sections or parts of trees examined. There may be

room for serious question, certainly room for basic experimental work, whether the cambium can remain inactive as regards cell division throughout an entire season; that is to say, the cambium ceases division at the end of one growing season over the entire stem and does not resume until the start of the second season later. In many cases observed by the writer, the cambium did lay down new xylem cells whose detection required the high-power microscope and complete and at times serial sections. Can the physiological processes remain in the, so-to-speak, neutral condition of respiration only, with no new cells on the one hand and avoidance of death on the other?

Douglass (1946*a*) has referred to missing rings many times. One of the problems mentioned by Hawley (1939) was "the location of missing rings on specimens growing in locations so difficult for life that no growth was possible during dry years . . .". One is tempted to ask, Should we use trees growing under such conditions? Or again, Do normal trees in normal distribution grow in such situations? Schulman (1945*b*) has been much more conservative and hence may be physiologically closer to the truth. Yet he has said: "It has been well established that, with sufficiently severe growing conditions, the cambium in various parts of the stem may 'go hungry' throughout an entire growing season and no new cells of wood may be laid down". Can the cambium go hungry without deleterious effects? Later he said (1951) that in "severe years much of cambial area may be entirely inactive in terms of new cell growth". This to botanists may need further work. Surely such a statement should be based upon an inspection of a high percentage of total cambium area. In Texas, Schulman (1951–52*a*) found locally absent rings to be very common, based upon core samples. A number of cores had no outside rings, although they were taken in November. How was this ascertained?

A cambium inactive over a long interval (if that is possible) brings up the question as to the causes, the mechanism and the possibility of death. Severe growing conditions have been cited above. Perhaps death of roothairs (Caldwell, 1913) is of importance. According to Kramer (1950), wilting caused injury or destruction of roothairs and the stopping of root elongation. Recovery was slow. Work of this kind with trees may be called for.

Fowells and Kirk (1945) clipped off the root tips of seedlings and found their survival rate lowered. Mowat (1947) pruned ponderosa pines to an extreme degree and reported apparent vigor little affected. When trees were chilled down to a few degrees above freezing for a whole season they still produced xylem rings (Handley, 1939), the chief effect being that the growth layer to a depth of four or five cells from the cambium was unlignified and the cell walls unthickened. Defoliation (Church, 1949) may cause suppression of rings, and at times three years of growth may be lacking on parts of the trunk in balsam. In spruce that recovered there was no indication of missing rings. Recovery took 12 to 15 years. However, trees may die six to ten years later because the rings are so narrow they can not " transport the required amounts of water to the crown ". Here again death may have been partly due to the death of absorbing rootlets. MacAloney (1944) worked on the management of jack pine in relation to root conditions, weather and insects. Vigor and condition of the trees used were important factors in amount of growth and in mortality. Defoliation by budworm was not of primary importance until the trees were otherwise greatly weakened. Rainfall records, from eight miles distant, showed ten years of about normal or better precipitation followed by 20 years of drought or near drought. Interestingly enough, " The growth in basal area in the best trees was progressively greater in each of the three decades considered, while that of the poorest ones decreased materially ". Feeding roots suffered great mortality during times of drought and high temperature, especially in 1936: " The death of the trees was very probably due, in the final analysis, to the drought in 1938 and 1939 ". Thus decadence and death of some trees were due to several causes climaxed by two years of drought. The other trees were vigorous and even gained in basal area progressively during two decades of drought. This work of MacAloney and of others in regard to drought effects through time is highly indicative. High mortality and forest retreat can be the consequences of short-time drought, especially where combined with other complications.

A step farther may be justified. Briegleb (1945) worked with ponderosa pine in Oregon and Washington, studying their responses as related to good and poor sites, and to low and high vigor: " Poor growth periods do not affect all tree classes to the

same degree". Briegleb referred to the poor growth years of 1929–1938 as described by Keen: "Trees of low vigor classes suffered a greater relative reduction in growth during the unfavorable period than did the more vigorous trees". Would this make for the so-called "sensitive" trees of some workers? But to continue: "Among the A- and B-crown trees the greatest reduction occurred in the older age classes, but among those having C and D crowns the greatest reduction occurred in the younger ages . . . . The effect of growth cycles is also more pronounced on poor sites than on the good". Briegleb found that growth of various stands varied widely, variations mostly accounted for by differences in site quality, stand structure and volume per acre. But small differences remained: "Whether the . . . differences are due to more or less permanent factors, such as climate, soil, or topography . . . is unknown".

Finally the work of Hansen (1938) must be mentioned. He worked with *Picea engelmanni* in Wyoming, where growing conditions were rather harsh because of thin soil, low soil temperature, high winds, and because of the fact that much precipitation falls as snow which melts and runs off while the soil is still frozen: "In these trees there is considerable ring width variation, and individuals also show considerable variation with one another for the same year". Growth layers, Hansen said, were commonly very thin: 0.05, 0.09, or 0.13 mm. for as many as 15 years. These rings probably "represent the minimum amount of growth which can take place and yet maintain life in the tree".

It seems clear that the problem of a cambium remaining inactive entirely or locally over a prolonged interval of years, or for one or two years, will bear further study. In summary, the point scarcely needs to be stressed that the physiology of tree growth includes highly complex processes and relationships, and can be neglected only at our peril.

TREE CLASSIFICATION. Foresters have classified trees for some time now on the basis of age and vigor in order the better to understand site quality, tree condition, volume yield and relationships in general between the tree and its habitat (Briegleb, 1945; Dunning, 1942; Gevorkiantz, 1947; Gevorkiantz and Olsen, 1950; Hornibrook, 1939; Keen, 1936, 1943; Pearson, 1946, 1950; Thomson, 1940; Wieslander and Jensen, 1946). It may not be out of the way to remark that an understanding of the forester's

point of view regarding age and vigor can be of great assistance to those working with tree growth in any of its phases.

GROWTH RECORD IN TREES

Perhaps this section should be entitled " How the growth record is used ". The remarks made about crossdating some years ago (Glock, 1941) apply with equal cogency now, and the writer would hesitate to add to the examples there given if it were not for the encouragement in the work of Dobbs (1951) and of Ruden (1945). Dobbs pointed out with great justification the over-simplification in much of the tree-ring work. For instance, we can well understand why he was disturbed when we read: " If you count the rings from the exterior of a tree back to its center, you discover not only the age of the tree but also the succession of wet and dry years through which the tree has lived " (Senter, 1938). Botanists and foresters, as Dobbs remarked, " have shown the least interest in the remarkable record which the tree leaves behind it in its wood. This is understandable, because it is they who are most likely to realize the complexity of that record ". One necessarily agrees with Dobbs. Tree-ring work has centered its attention on one ring character, its width, and on one climatic factor, rainfall. It may be that the statement of Dobbs, that " the width of the annual rings is one of the least reliable characters which could be chosen, either as an indicator of climatic change or as a means of identifying and dating individual growth layers ", could be enlarged to include growth layers from most habitats. A single feature, such as width of growth layer, may not adequately portray " the effects of a complex environment upon so complex an organism as a growing tree ". A table of ring widths or a graph of them " is a fantastically crude substitute " for the record embodied in the entire tree. As Zeuner (1951*a*) suggested, perhaps characters other than width may come to be used in tree-ring work in humid-temperate climates. This could well apply elsewhere.

In the matter of deriving past climates or predicting the future, the words of Landsberg (1947) come to mind: " An extrapolation leads to treacherous ground and even though it would take another half century to prove or repudiate a statement, the mental reservations are too numerous to make an attempt ".

Crossdating, or the matching of growth layers year by year

from one tree to another, has been held to be the vital key for deriving calendar dates and climatic records by workers in the Southwest. Trees or specimens whose growth layers do not crossdate are said to be erratic or non-climatic and hence are disregarded or rejected. If the approach were more from the botanical side, this insistence on crossdating would be more convincing.

CROSSDATING AS A CALENDAR BASIS

If crossdating were able to establish the annual character of a growth layer and if it were able to assure the true calendar date for each growth layer, we should have an ideal situation. Douglass as early as 1923 claimed that careful application of cross identification made dating of rings certain. In 1931 the same view prevailed. The same reliance on crossdating appears in the work of Antevs (1948), of Douglass (1946*a*), of Schulman (1945*a*, *b*, 1947, 1951, 1951–52*a*, *b*) and of Weakley (1943).

Antevs (1948) spoke of "absolute dates" obtained from tree-ring records and thus apparently accepted crossdating as the vital key. Schulman (1945*b*) used certain criteria to suggest the identification of false rings and then reached a solution by crossdating. In a discussion of the Colorado River drainage basin and its adjacent regions he stated: "It is obvious that there is throughout this transect of some 2,000 miles a tendency for persistence in chronology . . .". Such a statement is somewhat surprising from the ecologic standpoint.

In 1941 Douglass attempted to answer the criticism of Sampson (1940): "Our criteria of climatic character in the ring records in our trees is not sensitivity (the amount of fluctuation in thickness from ring to ring). . . , but crossdating quality which is of an altogether different nature . . . . Sensitivity is a secondary feature which is important only in the presence of crossdating". In spite of this he went on to say: "If there is no sensitivity there can be no patterns and therefore no crossdating by patterns . . .". It seems in other words that sensitivity is secondary to the feature for which it is directly responsible—a difficult piece of logic.

Will (1946) depended more upon judgment than upon measurement and dated rings within four or five years. Weakley (1943) depicted his chronologies on skeleton plots. Out of 400 years, 46 per cent showed below-normal growth.

Crossdating, as heretofore mentioned, has been held to prove the annual character of a growth layer. All trees or all specimens in a collection, however, do not necessarily crossdate. If growth-promoting factors operate to produce more than one sharply bordered growth layer per year on occasion, is it not possible that they do so in many trees of a stand (Glock, 1951)? Is it not more important to trace the course of growth by experiment and prolonged observation than to attempt to apply simple but arbitrary criteria, as sharp border and width of growth layer?

QUALITY OF CROSSDATING

The fact of crossdating is one thing, the quality is another. But before quality is considered a word must be said about the "eye and judgment" method devised by Douglass whereby rings are dated and crossdated by means of a handlens. Douglass has tried earnestly to teach his method to others, not always successfully. He learned to recognize by sight characteristic narrow rings, patterns of narrow and normal rings, and sequences. The method once grasped is rapid, reliable and, what is more, enjoyable. Not so to Gladwin (1940*b*) who called the method subjective: "There are some of us, however, who have run into difficulties and . . . the first question which arose to plague me was how to decide the elementary question of when is a ring narrow". The writer (Glock) has had the same experience as Douglass in teaching his method to students; most grasp the method rather quickly, but occasionally an individual does have difficulty. Gladwin devised a new method which employs all rings, but after consideration the writer prefers the Douglass method. So far as can be seen, the fundamental weaknesses, if such exist, are identical in the two methods. The Douglass method has seemed and does seem highly reliable for crossdating; its weakness lies in whether or not it establishes the annual character of a growth layer.

Bannister (1951) worked with Douglas-fir and ponderosa pine in the Gallina area, New Mexico. The graphs of the widths of five specimens show 21 parallel trends and 49 opposite—not very good correspondence. So far as the means of the two species are concerned he stated that their chronologies are essentially the same, and yet the graphs showed 58 parallel and 22 opposite trends. He compared his trees with those of Mesa Verde, 120

miles northwest. The Douglas-firs had 64 parallel and 26 opposite trends. The Douglas-firs of Mesa Verde versus the ponderosa pines of Gallina had 52 parallel and 28 opposite trends.

In Mesa Verde National Park Douglass (1942) took Douglas-firs from the side of a canyon, a site favorable to crossdating, he said. A span of 100 years taken from his chronology gave 73 parallel and 27 opposite trends.

Later (1946*b*) Douglass also reported on single trees from Mesa Verde. Two trees showed 50 parallel and 25 opposite trends; a different two had 56 parallel and 19 opposite trends. Seven trees showed 40 parallel and 35 opposite trends. Of these trees Douglass said: "This crossdating indicates climatic effects and gives a near record of precipitation in that region". Some will have difficulty in accepting the plain statement. Moreover, it is interesting, in view of the inconsistencies among the trees at Mesa Verde itself, to compare these results with those obtained by Bannister where he compared trees 120 miles distant with those from Mesa Verde.

Eidem (1943*b*) compared a curve of 14 trees from Trondheim, Norway, with a mean curve from Selbu, a valley some 50 km. distant, and obtained a correlation of 0.74 ± 0.05.

Friesner (1950) found mixed results in Indiana. Two members of the same species might have high agreement (i.e., 89 per cent), whereas another two might have low agreement. In the general picture he recorded agreements ranging from 22 to 89 per cent. Averages ranged from 46 to 62 per cent agreement.

Giddings (1941) gave graphs of tree groups from two to 500 miles apart in Alaska. In the "actual dating" of driftwood its graph showed 39 parallel and 26 opposite trends with one recent sequence, and 48 parallel and 17 opposite with another sequence. A comparison of the driftwood with both sequences gave 35 parallel and 30 opposite trends. The two wood sequences themselves gave 46 parallel and 19 opposite trends. So much for dating the driftwood. In so far as recent trees are concerned Giddings said that the same ring records existed as much as 150 to 200 miles apart. Two groups of five trees each, two miles apart, gave 41 parallel and six opposite trends, which is very good. Two groups of five trees each, 30 miles apart, gave 104 parallel and 34 opposite trends. A third group of ten trees, 50

miles away, added to the previous gave 29 parallel and 18 opposite trends. Two groups of 25 and 11 trees, 200 miles apart, gave 60 parallel and 40 opposite trends. When two groups of 28 and 10 trees 200 miles apart were compared with the previous groups 500 miles away, the results gave 29 parallel and 71 opposite trends. At best all of these results clearly indicate increasing divergence among trees with increasing distances.

Glock (1950) worked with tree cores from four species from the upper part of the ponderosa pine zone in northern New Mexico. Crossdating was practically nonexistent, and therefore measured ring thicknesses were compared. Expressed in percentage, individual trees in rather compact groups varied from 60 to 89 per cent in their agreements with each other. When the measurements were divided into two intervals, 1850–1897 and 1898–1941, the earlier interval always had the higher percentage of disagreement.

Hansen (1940) took cores from fir and spruce on the Medicine Bow Range of southern Wyoming and found crossdating relatively easy. However, the two species were only in "fair correlation" with each other: "Also the general trends from higher to the lower and from the lower to the higher points are somewhat in agreement". These are modest statements. In 1941 Hansen reported on his work with three species of conifers from central Washington. He tallied the years of agreement between each two species and found a variation from 37 to 41 out of 80 years.

Hustich (1945) used the novel method of correlating volume growth with radial growth and obtained a coefficient of 0.63 ± 0.14. In northern Fennoscandia Hustich (1948*a*) found coefficients of 0.74 to 0.83 for groups 140 to 190 miles apart, but when he compared this with trees from the coast of Norway the coefficients dropped considerably. He found (1948*b*) the curves of growth in Lapland and Oregon almost the reverse of each other, and apparently frowns upon such long distance correlations (1949).

Lutz (1944), who studied two species of swamp conifers in Connecticut, noted a close agreement of maxima and minima between his trees and those of Lyon from mesophytic sites.

Lyon (1943) studied conifers within a short distance of Boston, conifers chosen as typical of their sites. Graphs of two groups

gave trends with 74 parallel, 36 opposite, and 17 with one entry giving no change. For purposes of dating unknown sequences Lyon used a master calendar made up of maxima and minima in which practically every ring was noted. Six groups of eastern hemlock (Lyon, 1946) widely distributed over New England gave " somewhat uncertain " crossdating. A sequence of at least 100 rings to be matched against its own local chronology was judged necessary for dating.

Among conifers on the east coast of Hudson Bay near the forest-tundra border Marr (1948) found satisfactory crossdating between groups 80 miles apart. The incidence of first class narrow rings came out two in 159 years; second class gave eight. This resembles very much the character of the growth layers obtained by Glock (1950) centering at 9000 feet in New Mexico.

In Arkansas Schulman (1942*a*) chose trees from ridge tops. Junipers and pines taken from sites said to have poor drainage possessed sequences which were erratic and devoid of sensitivity; they were not used. Previous collections from the Mississippi Valley region, he said, had shown poor crossdating, and hence better field selection was needed. It is of interest to note that Schulman found most of the ring variation in the densewood, little in the lightwood: " The latewood curves . . . show that much of the crossdating in the total ring is traceable to the latewood ". Because of this he devised a " secondary index of growth ", the " inter-season or L/E ratio ". By inter-season does he mean between seasons or within a season (intra-season)? What do we have ecologically, that the densewood does not give us, when we obtain the ratio of densewood with character to lightwood without character? A test of the L/E ratio on six trees, 1860–1940, appeared to give very poor agreement. On the whole the results achieved with trees selected as above described must be viewed in the light of the work of Turner (1936*b*, 1937).

Schulman (1945*a*) worked with Douglas-fir and ponderosa pine in the Pacific Northwest. Nine Douglas-firs were compared with 17 ponderosa pines and the results spoken of thus: " In Figure 2 it is shown that Douglas-fir of the semiarid Northwest carries essentially the same chronology as ponderosa pine ". An analysis of the graphs of his Figure 2 gave 88 parallel and 54 opposite trends.

In his work on the Colorado River basin Schulman (1945*b*) covered a large territory. Graphs of tree growth were given for different tributary drainage systems; from these a test decade, 1851–1860, was selected for analysis with results as follows: Green River trees had three parallel and seven opposite trends; Colorado above the Gunnison, six parallel and four opposite trends; Gunnison, two parallel and eight opposite; Dolores, five out of ten parallel; and San Juan, four out of ten parallel. Schulman also assembled tree-growth records into mean curves for Douglas-fir, ponderosa and limber pines, and piñon, from the lower forest border. When analyzed the curves gave the following trend relationships:

Douglas-fir vs. pines	48 parallel, 12 opposite
Douglas-fir vs. piñon	43 parallel, 17 opposite
Pines vs. piñon	40 parallel, 20 opposite

Schulman (1947) collected extensively in southern California in order to extend gauge records of runoff backward in time. In bigcone spruce crossdating quality was at its best and the correlation coefficient between two of the trees came out 0.84. Among the five trees of the group, trend analyses ranged from 109 parallel to 94 out of 120 years. All five compared gave 84 out of 120 parallel. These figures are high when we consider the complex nature of tree growth, but whether they are sufficiently high safely to extend gauge records of runoff is a different matter. Collections also included groups of different species—white fir, western juniper, piñon, ponderosa pine and bigcone spruce. Inter-specific trend comparisons ranged from 67 parallel to 47 out of 80. When all five are compared the trends were 33 parallel and 47 opposite. Other groups, inter-specific and intra-specific, ranged from 54 parallel to 38 out of 80. When the five are compared the trends were 15 parallel and 65 opposite. A word must be said about what Schulman called "obscure chronologies", those showing poor crossdating because evidently they were "dependent primarily not on one element such as available water" but upon the entire complex of growth factors. Trend comparisons come out only slightly less favorable, if any at all, than those previously cited. Finally Schulman presented graphs as a transect for 1400 miles of the Pacific Coast in order to study possible systematic

shifts in dates of maxima or minima with latitude. " No reliable tendencies of this type were found ".

More comparisons of the same kind could be cited but one more must suffice. Schulman (1951) reported no significant relation between tree growth of British Columbia and that of Colorado River basin for the last three centuries, which is not unexpected. The correlation coefficient between tree growth of the Colorado River basin and southern California was 0.46, for 1650 to 1935, and between the tree growth of the Colorado basin and eastern Oregon it was 0.21.

In summary it will suffice to say that the examples of crossdating bear out the fact that tree growth varies from tree to tree and depends upon the interaction of a host of factors, internal and external. The examples illustrate what has been said before in relation to selecting a single feature, such as width of growth layer, to epitomize the total response of a tree to its environment. In the comparison of two growth layers, no matter where they may have been grown, there are only three possibilities: they are of equal width (where measured) or one is thinner or thicker than the other. Does crossdating solve as many problems as some workers maintain?

STATISTICAL CORRELATION

Caution in the use of correlations has been urged by various students (Dobbs, 1951; Glock, 1941; Jones, 1943; Lyon, 1943; Pearson, 1941; Sampson and Glock, 1942). Little need be added.

Jones quoted Keynes as saying that " sensible investigators only employ the correlation coefficient to test or confirm conclusions at which they have arrived on other grounds ". Glock (1942*c*) devised a method of correlating continuous time series by combining direction of variation from year to year with amount of that variation into a trend coefficient. Very probably a list of the number of parallel trends and of opposite trends gives a simpler and clearer picture of what tree growth and certain factors are doing from year to year. Lyon (1943) relied upon critical years only. Glock (1950), Hansen (1941) and Miller (1950) used essentially an enumeration of parallel and opposite trends.

In 1942 Schulman (1942*a*) refrained from using correlation coefficients and spoke of trends. In 1945 he (1945*a*) rejected the

use of the coefficients but gave values of r anyway because they are so well known. Another article (1945*b*) of the same year gave values of r apparently without comment. Later (1947, 1951, 1951–52*b*) he continued the use of correlation coefficients, which is not too objectionable if readable graphs are published.

The danger that correlation coefficients may be a hindrance instead of a confirmation of prior fundamental work is vividly emphasized in the following: "The result of this procedure is a correlation coefficient which indicates the effect of precipitation upon growth of that species in that area, and by use of it precipitation of the past before weather records were kept may be figured from tree growth of the past, with measurable percentage of certainty" (Senter, 1938). No better brake can be placed upon the possible misuse of statistics than the apt words of Dobbs (1951): "Fortunately, in the realm of tree-ring studies, the phase of inexpert or ill-considered resort to statistics appears to be on the wane". Statistics do not tell us things we did not know: "At most, it might justify a guess that rainfall and tree growth are not entirely unrelated".

CROSSDATING AS A BASIS FOR CLIMATIC INTERPRETATION

Crossdating has been held by some not only to establish the annual character of each sharply bordered growth layer which can be traced into more than one tree but also to establish a climatic record, especially either of rainfall or temperature. The technique embodied in collection and crossdating promote "long tree-ring indices of maximum fidelity to a single element, such as seasonal precipitation or runoff" (Schulman, 1945*a*). In fact "The ultimate objectives of the studies at the Tree-Ring Laboratory are (1) the mapping through tree rings of the mean seasonal atmospheric fluctuations year by year, for many centuries, over the entire world in all forested regions, and (2) the interpretation of such chronologies in terms of possible solar or other extraterrestrial forces and their use as aids in long-range weather forecasting". This surely was an ambitious program, and one wonders why botanists, foresters or meteorologists have not long since begun the same work. The answer no doubt has been given by Dobbs (1951) as quoted heretofore.

Concerning crossdating as a more or less magic formula, Dobbs

has said: "There is no more reason to suppose that trees which cross-date give a better picture of climatic variations than those which do not; on the contrary, they are more likely to give a distorted one, simply because they are selected for coincident features, some of which may well be non-climatic in origin". Such remarks are seemingly rather severe, but they come as a natural reaction to the insistence that crossdating is the key to all so-called tree-ring work (Douglass, 1941, 1945*a*, *b*; Hawley, 1941; Schulman, 1942*a*, 1943, 1945*a*, 1951, 1951–52*a*, *b*). Insistence on the climatic value of crossdating came out in the words of Douglass (1946*b*): "We found that the best ring records came from sites of limited and discontinuous water supply and that the identity of climatic trees was established by definite crossdating. Thus crossdating between many trees is itself the evidence of the climatic origin of the dating features".

Some workers have found that different species differed from each other in certain respects or that each had its own chronology (Burns and Irwin, 1942; Douglass, 1931; Giddings, 1941; Hawley, 1941; Huber, 1948; Lyon, 1943; Miller, 1950; Schove, 1950; Schulman, 1947). At places these differences are intraspecific. If two or more chronologies exist in the same area, which one gives a faithful record of climate? This was a problem which beset Miss Hawley (1941). A few of her statements were rather severely criticised (Glock, 1942*a*, *b*). When we are confronted by such a problem perhaps it would be better if we were to go back and begin with fundamentals, in this case the physiology of tree growth, rather than to proceed forward.

Attention almost exclusively to trees, which crossdate, from the lower forest border, and rejection of trees from near the forest interior (Douglass, 1941, 1946*a*) do not harmonize too well with the proposed program of mapping all forests of the world in order to obtain mean seasonal atmospheric fluctuations year by year (Schulman, 1945*a*). Apparently crossdating is at its best at the lower forest border where atmospheric factors fluctuate with a rather high amplitude. Even here the sites must be especially unfavorable. Douglass (1942) studied Douglas-firs on the side of a canyon in Mesa Verde National Park and noted the location as "an unusually dry site and one favorable to crossdating . . . in this dry area the precipices above and below, the

steep slopes of the grove area and the unfavorable tilt of the mesa above and the sedimentaries at the back of the grove, compel these trees to subsist on the precipitation that falls on their own area. The available water for the trees is close to a minimum". Again we read (Douglass, 1946*a*) of a tree "on a high isolated point or growing in a crack in a rock or thoroughly protected from any 'imported' water". These examples must suffice to indicate not only the insistence upon the lower forest border but upon very unfavorable sites such as steep rocky slopes within this dry area.

At first one is somewhat confused by the distinction between sensitivity of rings due to violent fluctuations in a growth factor and non-sensitive rings which have an erratic record. Schulman (1942*a*) spoke of groups of pines and cedars as being erratic and lacking in sensitivity, and therefore they were not used. In 1943 Schulman wrote "of violent fluctuations of ring widths (high ring sensitivity)" in trees whose rings were dated by crossdating. In 1945 (1945*a*) Schulman wrote more in the same vein: "in the dry Southwest the most useful chronologies are found in long-lived conifers of nonerratic growth characters situated on steep slopes underlain by pervious rocks, so that moisture conservation by the soil is at a minimum, and near the dry or lower forest border . . .". Farther along he wrote concerning sensitivity and asserted that "in cross-datable ring series the violence of the year-to-year fluctuations in ring widths is directly proportionate to the indicator value of the chronology". The more violent the fluctuations, the greater is the value. After careful consideration the reader concludes that a sequence which has violent fluctuations is sensitive if it can be crossdated, but erratic if it cannot be so crossdated. This sounds extreme and one really doubts that Schulman meant to go so far. Contrary to the concern of Douglass (1946*a*), the people of the eastern seaboard may not be unaware of the dryness of the Arizona region, of the effects of two rainy seasons a year, and the principles governing the income, retention and outgo of soil moisture.

Exclusive adherence to the process of crossdating has very nearly restricted the workers in the Southwest to lower forest border trees, trees growing under conditions adverse even for such a zone. Yet others, notably Burns, Dobbs, Daubenmire, Friesner, Glock, Hansen, Hustich, Huber and Lyon, have achieved

a measure of success at least from the ecologic standpoint in their studies on trees from more normal sites and from more humid climates. Hawley (1941) has grasped the fact that in all probability trees in the more humid regions are sensitive to environmental changes under which they grow in much the same fashion as those growing in the drier regions. Friesner in Indiana and Lyon in New England have made worthwhile contributions to our fund of botanical knowledge. Glock (1950) studied tree growth at the upper part of the ponderosa zone well within the forest interior and found close correspondence to growing season rainfall. He chose normal trees from sites normal to the area: " . . . the locations were chosen so that abnormal drainage toward or away from the trees was at a minimum". Steep rocky slopes with highly adverse conditions at the lower forest border were avoided.

CROSSDATING AND DATING APPLIED TO ARCHAEOLOGY

Hack (1942), in his studies of the physical environment in the Hopi country of Arizona, accepted tree-ring dating apparently without question. In addition he referred to droughts as revealed by tree rings; but other factors besides a lack of rain can restrict tree growth. Schulman (1948*b*) worked out a tree-ring index in the Uinta Basin of Utah back to 379 A.D. with the help of ancient beams. This index, he said, ran essentially parallel to the indices from Arizona. Will (1946) in North Dakota based a master sequence on one oak.

The whole matter of dating by tree rings is of much concern to archaeologists because they must be sure of the botanical foundation of tree-ring dating, of the method of extending master charts into the past, and of the method of crossdating an unknown by means of the master.

Hawley (1939) had experience with charcoal fragments averaging not over one inch in diameter and containing from two to 100 rings. Pieces with less than 30 rings were useless. If one fragment showed bark, the rest could be dated. If no fragment was complete, " then there is no recourse but to hazard an estimate of the final date, based on examination of ring curvature and of the growth increment". This is dangerous ground; how can ring curvature indicate the number of rings *outside* the specimen and worn away? As to dating onto a master chart, Hawley (1941)

stated: " All that can be said about the actual date of any set of specimens which cannot be matched into a master-chart is that they must antedate the earliest period represented by that chart ". Such a conclusion will be a surprise to ecologists. In the same report Miss Hawley revealed that pine and hemlock of the same area did not crossdate. It is difficult to reconcile the two statements. She did say that dating by one specimen is unsafe, and yet one master chart was based on one oak specimen from 1536 to 1659. Smiley (1951) had this to say: " In spite of the fact that many prehistoric sites are located near or on the forest border, the percentage of dated specimens is very low in ratio to the total number of specimens collected. Species of undatable quality were often used in construction as were trees of a datable species which grew under conditions that did not allow the recording of precipitation changes. It is estimated that between 5 and 10 percent of the total specimens collected have been dated ". It seems that Knipe (1942) dated a specimen of pine charcoal from a site in southern Arizona as 1243 to 1274. The piece contained 32 rings and was dated on the basis of the rings for 1263 and 1269 which were preceded by four large rings forming a strong " signature ". Colton (1945*a*, *b*, 1947) found it necessary to revise the date of the eruption of Sunset Crater in northern Arizona from 875–910 A.D. to 1046–1071. Tree rings and pottery types were used in conjunction.

In 1932 Gladwin (1940*a*) attacked the problem of tree-ring dating and became sceptical not only of what he called the subjective methods of Douglass but also of the validity of much of the dating. His results have been published in a number of articles (1940*b*, 1942, 1943). Antevs has given a review of another work (1946). Soon after 1936, Gladwin stated that Flagstaff dates were " brought into question " (1942) and he objected to the method of assigning outside dates to specimens lacking outside rings. Gladwin (1943) doubted the accuracy of dating specimens on a small portion of a master chart hundreds of years long. He was of the opinion " that the pattern of tree growth is often repeated over short periods of 25 years or so, and it is quite possible that such repetition may occasionally be of longer duration . . . . As I have said before . . . I have more faith in archaeological evidence than I have in tree-ring dating . . .". Because of the possible recurrence of ring sequences, Gladwin suggested the use of archaeological evidence to determine the general age of the

period and then the use of tree rings to give a more exact date within the period.

Until we know more about the course of tree growth within a season and from season to season, the factors internal and external that motivate growth, and the accuracy of the methods used in setting up a master chart, the Gladwin method appears to be a sensible and just expedient. But it also assumes a master chart of absolute accuracy.

RADIOCARBON DATING TESTS

Age determinations by radiocarbon analyses have been made to a greater and greater extent during recent years. To mention a few who have given attention to method and trial dating there are Deevey (1952), Flint (1951), Flint and Deevey (1951), Libby and Arnold (1950) and Zeuner (1950*a*, 1951*b*). Various cautions have been put out by Bartlett (1951), Childe (1950) and Flint (1951).

An interesting aspect of the dating comes out in connection with the analysis of certain tree-ring samples with which the present writer is acquainted. If the radiocarbon dating is very nearly correct and no contamination has occurred, the age of the sample is highly suggestive. A specimen of Douglas-fir wood obtained by Morris in 1931 from Red Rock Valley in northeastern Arizona was analyzed (Arnold and Libby, 1949, 1951) and gave an average age of 1042 ± 80 years, whereas the age based upon tree rings was 1370. Arnold and Libby (1951) commented: "Looks low versus expected 1370". Reference to the ages of other samples (1949) determined shows that the radiocarbon ages very nearly equalled or exceeded the expected ages. Only the tree-ring sample showed such a low age in comparison with the expected. Although the difference may not be statistically significant, one wonders about the accuracy of the tree-ring master chart which was built up on many specimens (in most cases) from trees that grew at the lower forest border. This is the environment where adverse conditions prevail, where high amplitude fluctuations characterize rainfall, soil moisture and other growth factors, where the greatest sensitivity exists, and where cross-dating is at its optimum. It is also the zone where it has been found (Glock, 1951) that multiplicity is a characteristic feature of

the annual increment. Glock has estimated the multiplicity at zero to 15 per cent with an average of five or six per cent, on the basis of trees growing away from the lowest forest border, and therefore those trees may have had less multiplicity than some of the materials procured by the Indians and later used in construction of the master chart. It is conceivable that further study will show that the quality of crossdating up to a certain optimum is directly proportional to the percentage of multiplicity.

GROWTH AND CLIMATE

No very startling results have appeared concerning tree growth and climatic factors since the first review (Glock, 1941). A few investigators have published rather extensively on climate as derived from tree rings, whereas the vast majority of botanists, foresters and ecologists has been primarily interested in tree growth as such and the factors, external and internal, which regulate it. It is rather generally agreed that soil moisture, because of its wide fluctuations, has great importance to trees near the borders of arid lands and that temperature during the growing season, because of its impact on physiological processes, has great importance to trees near the borders of cold regions. Nor should the probable role of growth-promoting substances be entirely neglected.

Particular emphasis has been given by some to the accuracy with which the widths of tree rings record rainfall. Whether or not such a position is justified will perhaps become apparent later. For instance, Douglass (1941) claimed that "If many independent trees in a forest over a wide area and for a long interval of time show similar ring variations in identical years, the cause of such variations is climate because climate is the common continuous factor in their surroundings". If we are not mistaken the area referred to is over hundreds of miles and refers especially to rainfall. How this fails to harmonize with the variations of habitat factors, even in short distances, is difficult to understand in the light of much ecologic and meteorological work, as, for instance, that of Croft and Marston (1950), of Visher (1946, 1950) and of others previously cited. Dobbs (1951) has given us an extremely penetrating and lucid analysis of the difficulties inherent in the use of simple ring widths as true

records of single factors and has listed many factors which may intervene at any point from rain to cell formation to affect the growth processes: "Even in a dry climate the relation between rainfall and the activity of the cambium is far from simple and direct". Any drought sufficiently severe will of course limit cambial activity: "But it is another matter to assume that every narrow ring represents a drought, or that every broad ring represents a wet year". As a matter of fact, "At present the only undeniable record of climatic effect upon the wood is the frost ring . . .". Much of what Dobbs says is highly pertinent, but lack of space forbids further elaboration.

Douglass (1946*b*) extended his claims by stating that growth curves "supplement the observed meteorological data by providing . . . a length of record many times that of the longest meteorological series . . .". Extension, not only into the past but also into the future, was proposed by Hawley (1939) with the further suggestion that amounts of rainfall might also be computed. According to Meyer (1951), statistical analysis indicated that 90 to 95 per cent of yearly growth variations were due to weather. Trees near the dry lands (Schulman, 1945*a*) are "natural gauges" which continuously record "fluctuations in annual precipitation and runoff", and those near Arctic regions are "living thermographs". No one apparently has ventured further than this.

The complexity of the relationships has been mentioned by Brooks and Kelly (1951), Lyon (1943) and Marr (1948). Meissner (1943) in Germany and Pearson (1941) in northern Arizona found no or little relationship between rainfall and tree growth. Graves (1946) described the complications in the weather of an unusual spring in northeastern United States with its early warm period and subsequent cold wet interval which caused root rot and a blight on one species. In central Europe Huber (1948) reported that rings are narrow both during dry summers and after cold winters.

Hustich (1948*a*) has done much of his work at the northern forest limit in Europe. There "the trees react closely to the smallest changes in climate". He has introduced what he called the climatic hazard coefficient (1947, 1948*a*, *b*, 1949) which is the degree of variability in growth caused by annual changes in climate. The coefficient in percentage is essentially the standard

deviation divided by mean temperature of the particular period. Hustich found that the coefficient decreases from north to south in Finland. Brier (1948) commented on the work of Hustich and emphasized a possible correlation between tree growth and mean annual hemispheric pressure.

In his careful synopsis of tree-ring work, Zeuner (1951*a*) has well summarized the problem: "Thus there is no doubt that temperature and precipitation do influence the growth of trees to a certain extent, though not exclusively and not everywhere in the same manner. A great many tree-ring records, in fact, show no distinct relations between precipitation or temperature, and the thickness of the rings".

GROWTH AND TEMPERATURE

For some reason temperature correlations do not seem to be so attractive to workers as do those of rainfall. None the less, positive results in any region would have a usefulness equalling that of rainfall correlations. Cook (1941*b*) found little relation between tree growth and either temperature or rainfall in eastern New York.

For a number of years Friesner carried on fundamental research in tree growth in Indiana, and we are indebted to him for much sound information. In a summary of a portion of his studies Friesner (1943*b*) remarked: "Temperature plays its most significant role in determining the time of initiation of growth but shows only an obscure and indirect relation to the quantity of growth. Of course, it must be remembered that the response of the organism is to the sum total of its environmental conditions and that temperature is a part of this total". In lower latitudes the relation is mostly inverse, whereas it is direct in the higher.

The following work has found a relation more or less between tree growth and temperature. It has been reported that Akerhielm (1940) noted that a small increase of temperature brought about a remarkable increase of radial growth of old pines in the north of Europe.

In Norway Eidem (1943*a*) held temperature of the growing season to be a leading factor in determining ring thickness in fir. Neither summer rainfall nor the preceding winter rainfall had an appreciable effect.

Giddings (1941) in Alaska was troubled by finding more than

one chronology. A spruce chronology on a gravel terrace differed from surrounding trees and gave a radical departure from the usual climatic reaction, being due perhaps to a combined rainfall and temperature effect. In contrast a different chronology—from timberline—gave good agreement with summer temperature. Trend analysis between June temperature and tree growth showed 21 parallel and eight opposite. Mean June temperature and a group of trees from Noatak had 17 parallel and 11 opposite trends; another group of 25 trees from Norton Bay had 17 parallel and 11 opposite trends. In comparison June precipitation and Norton Bay trees gave 14 parallel and 14 opposite trends. If temperature records could be made to match more closely the exact time of growth for the trees of the different chronologies (i.e., timberline and valley bottom), better correlation might be obtained. Later Giddings (1951) reported on two groups of spruce trees 50 miles apart and 80 miles from the weather station. The two groups showed 31 parallel and nine opposite trends. Compared with growing season temperature, June-July, each group gave 20 parallel and 13 opposite trends. Correlations of single trees were not very good. Perhaps when single trees are merged into an average, disagreements cancel out.

Hawley (1941) measured 23 pines, some of which came from central Georgia, others from southern Missouri, eastern Tennessee and Arkansas, and correlated them with yearly temperature at Cairo, Illinois. The coefficient, *r*, came out as 0.57. For oaks, *r* was –0.35. The negative correlation was surprising.

In reporting on the work of a student, Huber (1948) said that ring widths in the high mountains of Bayern correlated with mean summer temperatures, with mean noon temperature during the summer, and with duration of sunshine.

Hustich (1941, 1948*a*, 1949) has clearly shown the effect of temperature in northern Finland. From 1933 to 1939, radial and height growth, and needle length of *Pinus silvestris* followed the mean temperature of the warmest month (1941): "At the northern pine-limit the temperature is the most important impeding factor" (1948*a*). Even a fairly small increase in temperature appeared to cause "remarkable rejuvenation" in the radial growth of old pines at the timber line. Hustich presented correlation coefficients to substantiate the temperature relations. Growth of pine cor-

related with temperature 130 miles away gave: for June temperature, 0.14 ± 0.17; for July temperature, 0.54 ± 0.12; for August temperature, 0.31 ± 0.16. For July the coefficient is "fairly good"; but other factors must be considered, such as the effect of temperature during the previous year on food reserves, leaf surface and seed production. Hustich understood the complexities of growth: "The radial growth of the pine is, however, not a simple consequence of the temperature of the summer months in which the annual ring in question is formed". For tree records closer to the weather station, Hustich obtained radial growth versus July temperature, $r = 0.86 \pm 0.06$; cubic growth versus July temperature, $r = 0.61 \pm 0.14$. The difference between radial growth and cubic growth is of interest; correlated they gave 0.63 ± 0.14. As a summary Hustich said: "Generally speaking, in the northern part of the temperate zone the correlation between temperature and growth is stronger than the correlation between precipitation and growth". One can scarcely object to such a conservative statement. How well the trees give us an accurate temperature record through the years is a different matter.

Ording (1941) has done much work in Norway. Analyses were made on 130 trees of *Pinus silvestris* from six moor and swamp localities and on 50 pines and 90 of *Picea abies* from five productive forests. Correlations with temperature records from 1821 to 1920 showed wide rings of spruce and pine in warm summers and narrow rings in cool summers. But exceptions were frequent. Temperature of the preceding summer may also have an influence. Standard scales, Ording recommended, should be built for each species and for individual climatic regions. Spruce and pine in the same stand did not crossdate.

Schove (1950) has worked with tree growth in Scotland and has obtained important results. Dating by means of tree rings had three limitations at the start: it should be confined to one species at a time, to one climatically uniform area at a time, and should be corrected for age by a single objective method. In Scandinavia and in Scotland, rainfall and snowfall regimes vary considerably from place to place, and there was difficulty in crossdating pines near one fiord with those of a neighboring valley. More than one tree-ring series must be constructed. All this, he said, is somewhat different from North America where the geog-

raphy is relatively simple. It is indeed surprising to learn of this simplicity. Schove presented a mean growth curve for Swedish Lapland and northern Norway with which he compared a graph of the mean temperature anomaly of the growing season, May–August, at Trondheim. Analyzed, the graphs showed 74 parallel and 26 opposite trends. In reference to distant correlations, Schove said that many attempts had been made but they have invariably proved unsuccessful, as is to be expected, because correlations between weather factors are also very small.

GROWTH AND RAINFALL

By and large rainfall is the factor preferred in correlations with tree growth. Rainfall records are rather widely gathered, apparently accurate in amounts, easily understood in a quantitative fashion, and easily adjusted for use. Many points having to do with the selection of one factor as dominant in the growth picture have been mentioned before. It seems necessary, however, to mention the work of Foster (1944) in the Middle West on the discontinuity in the areal correlation of annual precipitation. He found high correlations over rather long distances in an east-west direction but low correlations north-south. Dahms (1942) learned interesting information on the effect of weather conditions on chinch bug abundance in Oklahoma. Light infestations occurred in years when the rainfall for the period from July 10 to August 20 of the preceding year was low. Something of this nature in tree growth could give us false correlation with rainfall of the previous summer.

Not all workers have met with success in attempted tree growth-rainfall correlations. Cook (1941*b*) found very little relation in eastern New York State. In Wyoming Hansen (1940) studied spruce and fir on the east slope of the Medicine Bow Range. No correlation existed between ring growth and annual precipitation at Laramie, 35 miles to the east and at a lower elevation. In the north of Finland Hustich (1948*a*) reported little relation to rainfall. At a distance of 130 miles between rainfall and tree growth correlations were: for June rainfall, $r = 0.08 \pm 0.17$; for July rainfall, $r = -0.24 \pm 0.16$; and for August rainfall, $r = -0.08 \pm 0.17$. For trees and rainfall close together, r for June–September rainfall was -0.19 ± 0.13. In northern Pennsylvania Meyer

(1941) obtained no significant correlation between growth and rainfall. In a letter to Glock dated April 7, 1942, Reed said: "So far as Iowa is concerned, I am inclined to believe that there is very little relationship between rainfall and tree rings". Weck (1944) in central Europe apparently found no correlation between basal area increment and precipitation for the same year and poor correlation between increment and the precipitation for the preceding four years.

Many workers have found a rough, essentially qualitative relation between tree growth, as measured by width of annual ring on a cross section, and rainfall, measured at a gauge over different intervals of time. In a study on climatic changes Antevs (1948) pointed out that the usefulness of tree-ring records is limited because of the "fact that the radial growth of trees used is determined by the winter and spring (October–June) precipitation, little if at all by the summer rainfall . . .". The reason may be valid but the facts in the reason may not be so iron-clad. As it stands the statement is a trifle strong.

In 1923 Douglass reported agreement between tree growth and local rainfall at Prescott, Arizona, of 70 to 85 per cent, depending upon the use of a conservation factor. Little has been done in the 30 years since then to improve the amount of correlation or the methods employed. Perhaps restriction to the lower forest border which "separates the successful forest from the desert" (Douglass, 1931) has prevented not only improved results but also a better understanding of the course of growth.

In Australia Fielding and Millett (1941) reported that summer rains have an important influence on annual diameter growth.

The extensive work of Friesner in Indiana has emphasized the role of summer rainfall, although he recognized clearly that "The relation of growth curves to rainfall is not a simple one" (Friesner and Friesner, 1941). The highest percentage of correlation between 17 specimens of *Quercus borealis maxima* and rainfall existed for the period June–August, and these percentages varied from 48 to 74. Lowest correlation commonly was between growth and total annual rainfall. Six specimens of *Fraxinus americana* correlated highest with the same period as did the oak and lowest with annual rainfall. Correlation percentages with June–August rainfall varied from 61 to 77. By studying intervals

in which rainfall had increased over the previous year, Friesner and Friesner found that an increase of three inches in June brought a like response in 72 per cent of the cases, the highest of any interval. When rainfall for November–October was ten inches less than the preceding year, the percentage of years with reduced growth was 82, the highest: "The important factor is whether the reduction in rainfall follows a year when rainfall was above normal or a year when it was about or below normal". When individual trees agree among themselves from 90 to 100 per cent, growth and rainfall have similar trends. Such trend correlation was perfect for June–August rainfall except for 1922, 1923 and 1931 (out of 1900–1939). During these three years the rainfall of August–July gave perfect correlation.

In 1950 Friesner reported the trend agreement between growth and rainfall shown by six species of hardwoods from Indiana. The results paralleled to a great extent his former work. On the whole the trend relationships were not high. *Carya ovata* gave the highest agreement, 68 per cent, when compared with rainfall for May–July, but the range of agreement for 23 different rainfall periods was from 51 to 68 per cent, not drastically significant. *Carya glabra* ranged from 46 to 55 per cent for 23 periods. Three periods, May–July, June–May and August–July, had 55 per cent. The results for four species were comparable with emphasis on the spring and summer rainfall.

Friesner and Friesner (1941) obtained like results with six species from Indiana. Highest agreements were with growing-season rainfall and lowest as a rule with annual rainfall. These results, favoring as they do the importance of growing-season rainfall, have particular significance because Indiana certainly can not be said to have a dry climate.

Glock (1950), working with conifers from near the forest interior of northern New Mexico, found greatest trend agreement (96.5 per cent) between growth and rainfall for March–July of 1909–1941. This he said was "consistent with the principle of maximum correlation with minimum-length month-interval". The rainfall station was at a distance of five miles. With a more distant and longer rainfall record he found higher agreement for the interval of 1898–1941 than for 1850–1897. These results along with other criteria indicated a change in amount of rainfall or in its nature (see Leopold, 1951).

Hansen (1941) used the trend method of agreement in his work with three species of conifers from central Washington. The number of years of positive trends out of 36 were: with annual rainfall, all three species, 8; yellow pine, 14; western larch, 19; and Douglas-fir, 22; with March–August rainfall, all three species, 9; yellow pine, 11; western larch, 19; and Douglas-fir, 23. Certainly these agreements are none too high.

In the Mississippi Valley Hawley (1941) correlated pines with annual rainfall for a coefficient of 0.52, oaks with annual rainfall 0.33, and cedars with annual rainfall 0.65. The 23 pines used came from an area of many hundreds of square miles and were correlated with Cairo, Illinois, rainfall. Graphs were constructed (Glock, 1942*b*) for the purpose of deriving trends. For the years 1880–1930 there were 23 cases of parallel trend, 11 cases parallel but relationship slight, and 16 cases opposite trend. The same methods applied to 15 oaks gave 22 cases of parallel trend, six cases parallel but relationship slight, and 22 cases of opposite trend. "Cedar" growth compared with an unnamed rainfall station some 50 miles distant gave:

Calendar year

Growth vs. rainfall ..... 14 parallel, 8 opposite
Growth vs. runoff ..... 12 parallel, 10 opposite

Water year (November–October)

Growth vs. rainfall ..... 13 parallel, 9 opposite
Growth vs. runoff ..... 11 parallel, 11 opposite

These are poor relationships. As regards correlation coefficients given by Hawley, she said: "Correlations were computed for the 22 year period of 1911–1932, excluding the year 1920 in precipitation correlations, for which year the data are erratic". If by chance 1920 was in high disagreement with growth then one is sceptical about its omission. We regret the absence of a complete explanation. A fuller review of Hawley's work is omitted here because it has appeared elsewhere (Glock, 1942*a, b*). However, one more point must be mentioned.

Miss Hawley tried to find homogeneous relationships over the vast territory of the Mississippi Valley. We are confronted with misgivings in the following: ". . . a lengthy drought indicated in the central Mississippi chronology must have been reflected in droughts on the Great Plains, although it is possible that on the

Plains the droughts may have been misplaced (*sic*) a year or so .... The fact that the modern droughts of 1934 and 1936 were so devastating in the Plains as well as in the central Mississippi indicates that a very dry period is likely to cover both districts at the same time . . .". Reference to the work of Hoyt (1938) showed that Miss Hawley was right for 1936 and 1934 and also for 1894, but partially or completely wrong for the remaining eight out of 11 years of major drought. Thus there is grave danger in drawing sweeping conclusions on meager data.

Huber (1941) constructed a rainfall calendar for pines in central Europe and another one for fir and oak.

Lyon (1943) compared conifers with rainfall in the vicinity of Boston. Hemlock correlated with May–July rainfall three miles distant by 53 positive trends, 24 negative, and six with no trend. On the whole the best correlations of pine and hemlock with rainfall were for the periods May–July and May–August. Lyon reported his comparisons on the basis of wide and narrow rings; for instance, in the case of hemlocks he used 52 out of a total of 81, 1856–1936. May–July rainfall thus showed 63.5 per cent positive, 13.5 per cent negative, and 23 per cent zero. Other rainfall intervals were not so good. For white pine and May–July rainfall the percentages were 63.3 positive, 22.3 negative, and 14.3 zero. Lyon is fully aware of the complexity inherent in both tree growth and rainfall. Secondary growth probably began in early May, and hence " the most important and consistent control of the growth increment is again shown to come through the growing season ".

Miller (1950) in Indiana analyzed two species of *Quercus* and one of *Fraxinus* in order to find what rainfall period showed the highest correlation with growth and which portion of the trunk gave the highest correlation. In all he used 23 rainfall periods of various lengths from a station ten miles distant. *Quercus alba* gave the highest trend coefficients with June–August rainfall, 75, and with May–August, 71. When all rainfall changes up to 40 per cent or greater were used, the coefficient rose to 83. *Q. velutina* gave the highest trend coefficients with June–July, 70, and with June–August, 70. *Fraxinus americana* gave the highest trend coefficients with May–August, 68, and with June–August, 60. In both the oaks the top areas of the trunks gave higher growth-rainfall trend coefficients than did the bottom areas: " This would appear

to indicate that annual growth in the top area of these species is more sensitive to rainfall changes than annual growth in the bottom areas". Intra-specific correlations among the trees of *Fraxinus* averaged 77; among those of *Q. alba,* 79; and among those of *Q. velutina,* 72. Individuals agreed better within their own species, except for *Q. velutina* which agreed better with *Q. alba.* In all, trend correlations among trees, between tops and bottoms of trees, and between growth and rainfall, were of about the same quality. Growing season rainfall was apparently the important rainfall for tree growth.

Miller (1951) also studied nine sections of *Acer saccharum* from Indiana and compared them to rainfall records 13 miles distant. The highest trend coefficient, 63, was with June–July rainfall. With 63 per cent positive trend and 37 negative, tree growth and rainfall did not agree too well.

Schulman has done a great deal of work in the dry Southwest; one must not forget, however, in spite of the emphasis on dry climate, droughts and adverse conditions, that where trees grow there is enough water for them. It is, then, not so much a matter of quantity of water as it is a problem of when and how often soil moisture is available—if the trees are present. Too little water for a year or two, and the trees die. In the Southwest the correlation coefficient between seasonal rainfall and annual tree growth was about 0.6 (1940*b*) over an interval commonly of 50 years. It may even be 0.8 or more in some cases: "The indication of the dominance of precipitation on growth on dry sites of the Southwest is very strong". In the present state of knowledge few would deny this, but, nevertheless, correlation coefficients, trend coefficients, visual comparisons, and above all an intimacy with the nature and processes of tree growth indicate clearly that rainfall, though of great import to tree growth, does not quite make that tree growth into natural rainfall gauges.

Since 1640 in the Southwest (Schulman, 1942*b*) four per cent of the years were characterized by extreme winter droughts with growth less than one-half of normal and about 15 per cent with less than three-quarters of normal. Summer rainfall had little effect. These may be important generalizations, especially if the annual increments were correctly determined in all cases. Another interesting point has been made by Schulman (1942*b*).

Trees under climatic stress of low rainfall may disagree with trees a few yards away not under stress, but they may closely parallel trees 400 miles distant. In this connection it may be well to refer to the work of Pearson (1944*a*) who compared the ponderosa pines of Arizona and New Mexico: " New Mexico forests receive less winter moisture, more during May and June, and a somewhat lower annual total than do the Arizona forests. The line of demarcation does not conform absolutely to the State line but nearly so ". Again Villeneuve (1946), remarking on climatic conditions in Quebec and their relationships to forests, said that a dry site tree in the north may be a wet site one in the south. These circumstances, in addition to what has been reviewed previously, are points of caution in long distance correlation. Schulman himself (1942*a*) realized the nature of the problem in his work in Arkansas: " It is certain that local variations in both tree growth and rainfall introduce fictitious (*sic*) discrepancies in the precipitation-growth relations . . .". Of much interest was his information that July–September rainfall was the most closely related of seven intervals with latewood growth. Occasionally entirely opposite trends were noted.

Weakely (1943) worked in western Nebraska where 80 per cent of the rainfall came April 1–September 30, with the greater part in April–June. A dry mid-summer might produce double rings. In spite of this distribution he correlated tree growth with annual rainfall. North Platte tree growth correlated with North Platte rainfall gave $r = 0.63 \pm 0.05$ for ring widths and 0.73 ± 0.05 for cross-sectional area. General tree growth correlated with general annual rainfall of the western part of the State gave coefficients which varied from 0.51 to 0.54. In some 400 years droughts average 12.85 years in length and no-droughts 20.58 years.

The results achieved during the past decade have been in general little or no better than those reported during the second decade past. Correlations have been more widespread but not more fundamental.

GROWTH AND RUNOFF

Anything which contributes to our knowledge of variations in stream flow, although lacking high accuracy, can be of much utility to problems of power, irrigation and conservation. In

recent years Schulman has worked diligently on collecting tree-ring samples to determine how well they represent stream runoff. Tree growth and rainfall are complex processes; runoff is no less complex.

In using runoff records for comparison with tree growth it must be assumed that there is a relationship between the soil moisture available to trees and the amount of water flowing past gauge stations in streams or that the two are influenced jointly by the same factor or set of factors. There is of course a relation between rainfall and soil moisture, and between rainfall and runoff. The complexities inherent in the rainfall–runoff relationship and in the rainfall–soil moisture–groundwater–runoff relationships are so great that it will be of interest to see what parallelism has been found to exist between tree growth and stream flow.

Lack of adequate knowledge of the entire province concerning runoff and the lack of space prohibit an exhaustive discussion. However, a few pertinent observations have come to our attention.

Cooperrider and Sykes (1938) have worked on the relation between rainfall and stream flow on the Salt River watershed above Roosevelt Dam in Arizona. The words of Cooperrider and Sykes, here applied to stream flow, sound very familiar from the growth and rainfall standpoint: ". . . the stream flow for any interval of time depends on many circumstances and factors and not alone on the amount of rainfall during the corresponding interval. Hence the extent to which any group of storms or the fall for some period contributes to stream flow is only vaguely revealed through general observations; neither is it definitely established through comparison of annual fall and flow records". Runoff from melting of winter snow may be protracted well into the spring: "The beginning and ending dates of the annual rainy periods vary greatly". In the summer, June–September, the storms are characterized by rainfall of high intensity. The two months of highest rainfall, July and August, contribute only slightly to stream flow, but that contribution is by means of direct surface runoff. In the winter, November–March, the storms are characterized by more general rainfall of low intensity. Its contribution to runoff is to a great extent through the groundwater percolation chain. April, May and October rainfalls are chiefly showers preceded and, followed by dry weather; "they are ab-

sorbed by the dry ground and over a period of years contribute but little to stream flow". When the percolation chain is well established, rainfall contributes heavily to stream flow. The base flow holds constant after the end of September and from then until January " there is almost no relation between rain and flow . . .". During the interval any changes are due to changes of temperature. Perhaps an excellent prerequisite to a study of tree growth and stream flow would be a thorough-going analysis of a drainage system similar to that made by Cooperrider and Sykes.

With some features of rainfall, percolation, and stream flow taken care of, Cooperrider and Sykes compared rainfall and stream flow. They reported a close relationship between average annual flow and winter rainfall during a 35-year period: ". . . the annual flow is more apt to agree with the winter than the average annual rainfall". Therefore, if both tree growth and stream flow respond to winter rainfall, tree growth should equally correspond to stream flow. In contrast to the above quotation, Cooperrider and Sykes gave the following overall summary: " In general, the trend of annual stream flow may be said to follow closely the trend of annual rainfall. In fact, the relationship is close when one considers factors like *seasonal fall, flow lag,* and *fall distribution,* which may determine how large or small a part of a given annual fall is returned in flow during the same year". The relationships are complex, a matter of which the writers of the quotations were well aware. Data of separate years showed mixture of lag and no lag. Rainfall distribution was complex. The year 1931 had the second highest fall in winter in 35 years, and yet annual flow was below average.

A comparison of rainfall and streamflow, 1902–1936, gave:

Annual trend	25 parallel,	9 opposite
Summer trend	27 parallel,	7 opposite
Winter trend	22 parallel,	12 opposite

Two of the 25 parallel, above, showed no change in rainfall from one year to the next, but showed a large change in flow; one of the 22 parallel showed the same change. The figures of trend given above, between rainfall and stream flow, are not too encouraging. Now we may report correlation coefficients given by Cooperrider and Sykes:

Annual flow vs. rainfall 0.79
Summer flow vs. rainfall 0.67
Winter flow vs. rainfall 0.81

Graphs showing accumulated excess and deficiency of rainfall and stream flow for the upper Salt River watershed gave 24 parallel, ten opposite. Another method of analysis was to examine the averages: 19 out of 35 winter rainfalls were above average, 16 were below. Ten of those having above-average rainfall also had above-average annual flow; 14 of the 16 with below-average rainfall also had below-average flow. It may be well to summarize the above matter in the words of Cooperrider and Sykes: " The ratio of stream flow to precipitation is never a constant, the amount of precipitation being only one of the factors affecting annual stream flow ". Over the drainage basin as a whole the total rainfall, 1902–1936, was 711 inches; total stream flow was 116 inches. Hence, 16.3 per cent of the rainfall was returned as stream flow. The right kind of rains may keep soil moisture high and yet give little to stream flow. One can conclude only that the subject of stream-flow relationships contains many phases and that it is indeed complex.

Croft (1946) analyzed water-supply factors in the inter-mountain area, and stressed mantle-moisture content. A wet soil increases runoff. In contrast, " Rainfall is not effective in producing stream flow, except as channel interception, after the soil mantle attains a definite capillary moisture deficit near the surface ".

Hansen (1940) was interested in growth and dominance in a spruce-fir association in the Medicine Bow Range of Wyoming but, none the less, gave consideration to runoff: " Most of the precipitation in the spruce-fir forest occurs as snow, and the amount of moisture lost through runoff and evaporation is not necessarily a function of the annual precipitation ".

Hoyt and Langbein (1944) have given us much information on the relationships of stream flow to different climatic factors. They announced at the start that " Stream flow is dominantly the integrated result of many diverse climatic factors ". Also, it is influenced by soil, rock, topography and other factors: " Stream flow has its origin in precipitation, but the portion that will drain from the land to the streams is conditioned by complex interrelationships still only imperfectly understood ". In addition to

such general statements, Hoyt and Langbein gave analyses of temperature effects and of the areal extent of excessive and deficient stream flow by years. This information is highly significant indeed in relation to correlations of tree growth over long distances. Stream flow is a natural measure of the net amount of water that escapes evaporation and transpiration: " Precipitation, representing the supply, is . . . fundamental, but its time distribution and influences of other climatic factors may substantially modify its effects ". Surely we must be able to cope with all the intricacies of soil moisture, groundwater hydrology and runoff before we can understand the devious course taken by the chain of relationships between tree growth and runoff.

A report by the Regional Forester (1951) for the Arizona-New Mexico region gave data on stream flow in three small mountain water sheds in central Arizona. Results corroborated those obtained by Cooperrider and Sykes in that the percentage of summer rainfall appearing as stream flow varied from 2.1 to 3.8 for the three watersheds, whereas the percentage of winter rainfall varied from 14.7 to 31.6. Little summer rainfall appeared in the streams.

Schiff (1951) also worked with small watersheds. At times more rainfall gave less runoff.

Thornthwaite (1945*a*) studied rainfall and runoff of the James River basin and the Great Valley of Virginia over a period of 31 to 37 years. Trend analyses were made of rainfall and runoff in the two regions. For the Great Valley there were 29 parallel, seven opposite trends; for the James River 22 parallel, eight opposite. A comparison of the rainfall of the two regions gave 27 parallel, three opposite; of the runoff 31 parallel, five opposite. The trends of the data for combined rainfall and runoff gave 20 parallel, ten opposite. Trend reaction for the two basins, regardless of the nature of the trend, gave 23 parallel, seven opposite. One can see the operation of factors other than rainfall in these comparisons.

With the above all too brief discussion of the complexity in runoff relationships we must pass on to some of the results obtained by attempts to correlate tree growth and runoff.

In 1941 Hawley compared " cedar " growth and runoff of the Norris Basin, and obtained $r = 0.61$ for annual rainfall and $r =$

0.56 for the water year of October–September. Search of the written report failed to disclose the location of the "cedars" and the particular stream whose flow was used as a measure of runoff. Because the graphs of the report are in a very unsatisfactory condition no separate analysis is here attempted.

In 1945 Schulman (1945*c*) reported a preliminary study of tree rings as an index of runoff on the headwaters of the South Platte River.

Schulman (1945*a*) reported rather extensively on tree growth and runoff of the Pacific slope. A complete reading of his work leaves an impression of over-simplification, although, if he had paid attention to all factors, his exploratory work would have been greatly increased. Exploratory work is necessary, perhaps to be performed even before the fundamental course of growth is understood.

Schulman gave graphs and data which included October–June rainfall at Durango, Colorado, Animas River runoff at Durango, Mesa Verde tree growth (seven trees), Rio Grande runoff near Del Norte, Colorado, and tree growth (one tree) at Wagon Wheel Gap, Colorado. Schulman gave correlation coefficients; the present writer made trend analyses of the graphs. Tabulated results give:

1. Durango rainfall vs. Animas River runoff—34 parallel, 6 opposite
2. Mesa Verde growth vs. Wagon Wheel Gap growth—63 parallel, 28 opposite
3. Durango rainfall vs. Mesa Verde growth—36 parallel, 11 opposite
4. Animas River runoff vs. Mesa Verde growth—30 parallel, 10 opposite
5. Rio Grande runoff vs. Wagon Wheel Gap growth—39 parallel, 12 opposite
6. Animas River runoff vs. Rio Grande runoff—33 parallel, 6 opposite

For No. 3 above: $r = 0.78$
For No. 4 above: $r = 0.73$

In relation to No. 1, Schulman said that rainfall was "obviously paralleled" by runoff. In relation to Nos. 3 and 4 he said that tree growth gave a "reasonably close index" of both rainfall and runoff. Because the two drainage basins are close together, "the chronology in tree growth (No. 2) and in runoff of the two areas (No. 6) is essentially identical". There is considerable latitude in the near identity.

There are many difficulties in the use of station rainfall records and gauge records of runoff when those records are distant from

the trees. We are faced with these disadvantages over much of the forested area, and Schulman (1945*a*) had to work against long distances. It is difficult to reconcile his statement: "The generally parallel march of fluctuations in precipitation at San Francisco and San Diego . . . indicates a general tendency to uniformity in annual chronology along some 500 miles of coast southward from San Francisco" with a trend analysis which gave 63 parallel and 29 opposite. Correlation of San Jacinto district tree growth with San Diego rainfall gave $r = 0.44$ and a trend analysis of 67 parallel, 24 opposite. The same tree growth correlated with Kings River runoff gave $r = 0.59$ and trend analysis of 24 parallel, 22 opposite; with San Gabriel runoff, $r = 0.57$, trend analysis gave 31 parallel, 15 opposite. Schulman fully realized the "dubious value" of such distant comparisons.

In his work on tree growth of the Colorado River basin Schulman (1945*b*) discussed the necessity of very particular methods of field selection of trees. He said: "Experience has shown the possibility of 'improvement of the data' by the repeated refining of field sampling criteria; this is a magnificent property of tree-ring indices, which in a very basic way cuts the Gordian knot of errors in the relationship of these indices to rainfall and runoff". This statement could be considered somewhat extravagant when it is compared to the change which has occurred from a previous statement (1941) which said: "Criteria for selection are based largely on common sense, plus a generous dose of practical experience".

Schulman took cores extensively over the West, including trees from the Green River basin, Colorado basin above the Gunnison, Gunnison River basin, Dolores River basin, San Juan River basin, Southern Utah, Salt River basin, Gila River basin, and southern Arizona. This was a tremendous project and should give a fairly good idea of the agreement not only between tree growth and runoff but also between tree growth and such rainfall stations as were available. The records of eight streams from British Columbia to southern Colorado were given; they ranged in length from 1890 to 1941 and 1911 to 1941. If all are compared regardless of length it is found that nine out of 51 agree in trend. For the North Platte, Colorado, and the Rio Grande, 20 out of 30 agree.

Results are none too encouraging among the tributary basins of

the Colorado system. Only a sample tributary will be given, the Green River basin. Two rainfall records, October–June, gave 20 parallel, ten opposite trends. Runoff compared with tree growth gave 19 parallel, 15 opposite. Tree growth compared with one rainfall record gave 16 parallel, 14 opposite, and with the other rainfall record 23 parallel, 17 opposite. This second rainfall record compared with runoff gave 23 parallel, 11 opposite. Five other tributaries showed comparable results. Concerning these comparisons Schulman said: "In spite of the obvious general parallelism in the rainfall-growth comparisons . . . , there are evident in almost all some apparent disagreements between the fluctuations in growth and those in recorded winter precipitation". No significant relation between summer rainfall and growth was noted and, further, there was no unqualified effect of summer rainfall on next year's growth. In all tributary basins Schulman found a "fair degree of correspondence" between tree growth and rainfall and between tree growth and runoff.

Southern California was given critical attention by Schulman (1947). A general parallelism was found in the seasonal rainfall over much of south and central California. A trend analysis of the seven stations recorded gave 11 parallel, 19 opposite. Comparison of each two stations gave trends ranging from 26 parallel, four opposite, to 19 parallel, 11 opposite. In the Coast Range tree growth versus rainfall gave $r = 0.65$, or in trends 29 parallel, 11 opposite. Tree growth versus southern Sierra rainfall gave $r = 0.58$, or in trends 28 parallel, 12 opposite. Tree growth versus San Gabriel River runoff gave $r = 0.61$, or in trends 28 parallel, 12 opposite. Tree growth versus Kings River runoff gave $r = 0.52$, or in trends 27 parallel, 13 opposite. Rainfall of the southern Sierra versus Kings River runoff gave 30 parallel and ten opposite trends. These figures are as significant for a comparison of the correlation coefficient with trend analysis as they are for the degree of agreement between tree growth and rainfall and between tree growth and runoff.

Schulman (1947) also gave inter-regional correlations but their significance does not justify extended discussion here.

In the Navajo National Monument Schulman's work (1948*a*) produced a growth record extending back to 698 A.D. Tree growth appeared to reflect the winter rainfall.

In a summary of his tree-ring work, Schulman (1951) correlated regional tree-ring indices with rainfall and runoff. Tree growth in each case which follows was correlated with the rainfall or runoff indicated. Colorado River basin: Colorado River runoff, October–September, $r = 0.66$; Eastern Oregon: Eastern Oregon rainfall, September–August, $r = 0.50$; Columbia River runoff, January–December, $r = 0.56$; Southern California: Coastal rainfall, July–June, $r = 0.65$; Kings River runoff, October–September, $r = 0.52$; San Gabriel River runoff, October–September, $r = 0.61$. Do these coefficients give us any direct information on the chances of parallel variation in any one year between tree growth and either rainfall or runoff?

Schulman (1951–52*a*) extended his activities to Big Bend National Park, Texas, where the available rainfall record lay 250 miles away at El Paso. Tree growth, he said, "tends to parallel" the march of winter rainfall. Trend analysis gave 39 parallel, 21 opposite, between tree growth and October–June rainfall. Perhaps the Big Bend trees "provide a better index of local rainfall than is evident" from the graphs because "the distance factor acts strongly in this region of variable and spotty rainfall". A collection was also obtained from the Guadaloupe Mountains 200 miles north-northwest of the Big Bend, and the growth record there closely paralleled tree growth from the Big Bend. Analysis showed 65 parallel, 25 opposite trends. A comparison of Guadaloupe tree growth with Carlsbad, New Mexico, October–June rainfall, gave 24 parallel, 16 opposite trends. Tree growth versus Pecos River runoff gave 21 parallel, nine opposite trends. Carlsbad rainfall versus Pecos runoff gave 18 parallel, 12 opposite trends. It seems clear that these figures do not show a strong parallelism.

In a progress report Schulman (1951–52*b*) adopts two innovations. The first and more important was the extension of the growth-rainfall relationship to the rainfall of July–June from that previously employed, the winter rainfall of October–June. Naturally such a relation would satisfy our fondest hopes—that tree growth records annual rainfall rather than that of the growing season. Perhaps, however, it is asking a great deal of trees to record moisture that passes through the soil when they do not use it actively. An intense desire to find an index of annual rain-

fall should obscure neither the quality of the evidence nor the methods whereby that evidence is obtained.

The scond innovation was the adoption of a coefficient of sensitivity. In 1928 Douglass defined mean sensitivity " as the difference between each two successive rings divided by their mean ". It gives in essence the degree of variability in a sequence and as such has high value in giving the fluctuations and inter-relations of growth-factor influences whatever they may be. Of all devices that give an insight into the vicissitudes of tree history, mean sensitivity seems to be the most revealing. Schulman has based his coefficient on mean sensitivity. This coefficient, R, is the ratio of group sensitivity to the average of single tree sensitivities. As we understand it, group sensitivity is the mean sensitivity of the merged growth record; the other part of the ratio is the average of the mean sensitivities of the trees taken singly. Thus, there is a re-use of data and trees are compared with themselves by a rearrangement of the figures representing their sensitivities. Does R have a functional value? What is its advantage over the mean sensitivity of Douglass? Schulman's data show an increase in the value of R with approach to the desert border. The drier the site (and the more violent the fluctuations in certain growth factors) is, the higher the value of R. But this is also what mean sensitivity shows (Douglass, 1928; Glock, 1937).

Schulman (1951–52*b*) asserted that a single radius often gave a remarkably faithful record of rainfall and runoff. One tree from Mesa Verde compared with Rio Grande runoff 100 miles distant gave $r = 0.68$; a second tree gave $r = 0.65$; and the average of the two trees versus runoff gave $r = 0.72$. Averaging apparently has the same effect as smoothing. One tree from near Pecos, New Mexico, compared with runoff of the Pecos River, and some 12 miles distant " from the weighted center of rainfall in that basin above the tree site ", gave $r = 0.78$; a second gave $r = 0.49$; and the average of the two trees gave $r = 0.72$. Aside from the questionable practice of using the correlation coefficient in continuous time series, what is obtained by such a coefficient? It means no doubt a certain amount of covariation during certain years. But it also means that in certain years tree growth varies in the same direction as the runoff: that runoff consisting of rainfall past and present which the trees did not and could not use.

Tree growth is compared with something that does not affect it, a rather round-about method. This does not mean to say that we should not grasp the opportunity of employing tree growth to reveal runoff if we can. Weakness must be recognized as well as strength. In the evidence presented runoff does not parallel tree growth year by year for all years; thus we obtain a general picture, not a detailed one. In reference to the four trees above mentioned Schulman (1951–52*b*) said: "These specimens are indeed highly selected; however, it is estimated that at least 20% of the trees under analysis have this order of fidelity to the appropriate rainfall and runoff series". The other 80 per cent, presumably, do not measure up to the quality or coefficient value of the 20 per cent, and that is subsequent to field selection. In the introductory paragraphs (1951–52*b*) Schulman remarked that he had begun work of a nature "to develop more secure interpretations of the ring records in terms of absolute values of past rainfall and river flow . . .". The results so far represent an enormous amount of work but are as yet not too encouraging in terms of the ultimate objective.

GROWTH RINGS AS A TOOL

Growth rings are not always used as attempted substitutes for gauges of rainfall or temperature or runoff. They have given the dates of certain events, and, because of the value of the method especially as developed in recent years by Lawrence, brief mention will be made of the work more as a matter of reference than as an exhaustive discussion.

The age of stands affected by glaciers, the time of ice advance, and the time of retreat have been closely approximated by counting the growth rings of the proper trees (Butters, 1914; Cooper, 1923, 1939; Lawrence, 1950; Lawrence and Lawrence, 1949; Mathews, 1951; Nichols and Miller, 1951; Sharp, 1951). Langenheim (1949) dated landslides in Colorado by means of the eccentric rings in trees tilted by the slides. In Texas, Roth (1945) counted the rings in trees perched on small erosion remnants in order to obtain the limits within which the last epicycle of erosion began. Hansen (1946) referred to charcoal logs buried by pumice from Mount Mazama; they suggested that the climate at the time of the eruption was similar to that of today.

CONCLUSION

A review and analysis of all material pertinent to tree growth are tasks of such magnitude that years of work would be required for their accomplishment. Without doubt important studies have been omitted unintentionally.

How well we have analyzed trends as listed in the Introduction the reader must judge. Two main points stand out: *a*) Investigation into the fundamentals of plant growth; *b*) attempts to use growth rings as natural gauges of temperature, rainfall or runoff. Much work yet to be done separates the two. In reference to the use of tree rings, Dobbs (1951) has said that "At present the only undeniable record of climatic effect upon the wood is the frost rings . . .". Even so, "It can scarcely be overemphasized that the whole history of a tree's growth in relation to its environment is recorded in its wood, and that it needs only the separation of the general from the special elements in that record to make it intelligible" (Dobbs, 1942). Fundamental work is never ended, and in reference to tree growth "extensive experimental studies under controlled conditions are desirable at the outset" (Sampson and Glock, 1942) and are as important today as they were ten years ago. If a review of the literature has given us one primary impression it is to the effect that tree growth will eventually be understood by an approach through plant physiology and anatomy, and conditioned by a knowledge of growth factors, internal as well as external.

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